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THE TERATOLOGY OF FISHES

BY

JAMES F. GEMMILL, M.A., M.D., D.Sc.

LECTURER IN EMBRYOLOGY, GLASGOW UNIVERSITY, AND IN ZOOLOGY,
GLASGOW PROVINCIAL TRAINING COLLEGE

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INSCRIBED TO MY HONOURED TEACHER

JOHN CLELAND, M.D., LL.D., D.Sc., F.R.S.,

EMERITUS PROFESSOR OF ANATOMY, GLASGOW UNIVERSITY,

NOT LESS IN AFFECTION AND ESTEEM THAN IN ADMIRATION

OF HIS DEEP INSIGHT INTO THE PROBLEMS OF TERATOLOGY

AND THE LASTING VALUE OF HIS CONTRIBUTIONS TO ITS STUDY

EMBRYOLOGICAL LABORATORY,
GLASGOW UNIVERSITY,
June, 1912.

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INTRODUCTION.

THE primary object of this Memoir is to throw light on the structural aspect of the major abnormalities occurring in fishes, particularly in the trout and salmon. Nearly half of the text, and practically all the illustrations, are devoted to this purpose. The Plate-figures consist of photomicrographs of sections and other specimens, and of reconstruction diagrams which, like the anatomical descriptions in the text, are based on the study of numerous series of sections. I have to express equal indebtedness and thanks to the Trustees of the Carnegie Bequest for the support which has made possible the publication of the work in its present form.

The greater part of my trout material was obtained some years ago from a Hatchery at Lochwinnoch, through the good offices of Mr. John Peden who was then in charge. Specimens were also received from the Loch Lomond Hatchery and from various private sources. In addition I had the privilege of examining at leisure the Salmonid material in the collection of the Royal College of Surgeons of England.

I desire to acknowledge indebtedness to the kindness and skill of my friend, the late Thomas Reid, M.D., LL.D., for greatly-valued assistance in the preparation of a number of the photographs. My best thanks are also due to Mr. J. G. Connell, F.R.M.S., for help in compiling the Indexes, of which there are three, namely, one of *Structures and Subjects*, one of *Fishes*, and one of *Authors*. The first includes full references to the various Plates and Figures in which individual structures receive illustration. It is through the courtesy of the Council of the Zoological Society of London that illustrations from papers of mine which appeared in their *Proceedings*, 1903, Vol. II., and 1906, Vol. I., have been reproduced in Plates XVII.-XX. and XXV., and this courtesy is herewith gratefully acknowledged.

Whilst, as stated above, the main content of the work is structural, occasion has also been taken to deal briefly with other aspects of major monstrosity in fishes, and to point out relationships with higher vertebrates.

In addition, the minor abnormalities form a large and varied group, many sections of which might well receive separate and lengthy discussion. My aim has been to describe these as briefly as is consistent with moderate adequacy of treatment, and to make it easy for future workers to get into touch with the chief present sources of information in each subject. It is hoped that this latter object has been attained through the literature-references and the Bibliography.

The study of monstrosities among fishes merits a distinct and important place in the biological field. Although this study has come latest in point of time, its data are now in process of incorporation with those of general vertebrate teratology, the foundations of which they have not failed to deepen and extend. The following circumstances favour this result: (1) In the bony fishes, which provide by far the greatest number of monstrosities, the ova are abundant and the processes of fertilisation and development take place outside the body of the parent. Plentiful material is available at all stages for observation and experiment. Facts of the greatest value have thereby been ascertained, particularly with reference to mode of origin and early development. (2) Although the major types of monstrosity in fishes do not survive the period of nutrition by the yolk sac, still at the end of this stage the cartilaginous skeleton and practically

all the other structures except the bony framework have been laid down in their final form, and already exhibit their adult relations. Each specimen examined thus provides us in small compass with a compendium for its type, the morphology and histology of which can be studied at the same time and from the same series of sections. (3) The vertebral column is of relatively great length, while the limb masses are small. Accordingly, in the most interesting types of monstrosity, namely those in which there is axial union of two or more embryos, we may expect to find the characteristics of such union exhibited in simplest form. The law that homologous structures become joined together, always holds good, and the full series of double and multiple forms in fishes provides us with examples in which "compositeness," due to primary or secondary fusion, is exhibited by practically every organ and structure in the body. (4) In the great majority of fishes segmentation is partial; we can speak of a circumscribed blastoderm resting on the yolk mass and giving rise at one part to the rudiment of the embryo. In these points there is correspondence with avian and reptilian development, and with those characteristics of mammalian ontogeny which indicate an ancestral highly yolked condition of the ova. Accordingly we find that in their major abnormalities the fishes show surprisingly close relationships even with the mammals.

From the general point of view the most interesting teratological questions are those which are concerned with *origin* and *causation*. A great deal of the data necessary for forming properly grounded views on those questions is still in process of accumulation. Meantime, I would venture to put forward the following propositions, from my reading of the available evidence, particularly as it has presented itself to me in connection with the teratology of fishes. The underlying ideas have long been part of the currency, if not of the accepted currency, of biological thought.

I. *Each of the recognised types of monstrosity, major as well as minor, can arise in a spontaneous or autogenetic manner, by abrupt germinal variation.* These terms are used with the meaning that (*a*) the results are not due to the action of environmental factors on the germ-cells directly concerned, or on the embryo itself; (*b*) should survival and reproduction be possible, the malformations tend to be transmitted to descendants. The course of ordinary epigenetic development must depend in the main on the nature and characters of the fertilised ovum. Although these are remarkably steadfast, there is evidence that along various lines they are subject to a certain measure of insecurity. Using terms of analogy, we may speak of *nodes of instability* in the intimate constitution of the germ-cells. The instability is not indeterminate, but tends in each case to open up definite teratological potentialities, and occasionally, from some unknown cause, one of these is followed instead of the normal course of development. The aberration may involve the whole organism as in duplicity or multiplicity, or it may only affect groups of organs or single organs, as in hermaphroditism, pug-head, various fin abnormalities, etc. Monstrosities which arise in this manner may be described as spontaneous or autogenetic.

II. *Most of the recognised teratological types, and particularly the major ones, are also capable of being produced by environmental factors acting during the course of development.* Malformations arising in this manner may be termed acquired, and there is no evidence that they are transmissible. It is obvious that the environmental factors in question are not causal in any real sense. They can neither supply motive power nor guidance in the production of any type. All they can do is to cause the course of development to deviate along certain lines which the organism or structure is capable of following. These lines were already marked out through the potentialities referred to under I. The latter are primary to, and indicate the limits of, the former. At the same time, as regards ordinary frequency of occurrence, it is quite possible that, for some types, the instances of *acquired* may outnumber those of *autogenetic* abnormality.

III. On the whole the two groups (namely those of autogenetic and of acquired abnormalities) tend to coincide with one another. At the same time the former will be found to have a wider content than the latter, if induced pathological conditions are left out of count, but here the boundary between teratology and pathology becomes difficult to define. In any case, *the fact that a particular abnormality appears spontaneously is an argument for, and not against, the*

probability that the same abnormality can be artificially produced. The converse proposition carries with it an even stronger degree of likelihood.

Teratological variation is thus not essentially different in kind from ordinary variation. Owing, however, to infrequency or non-survival or absence of reproductive faculty, the major teratological variations will not, as a rule, have any influence or evolution. That this is not always the case may be surmised from the facts relating to hermaphroditism (p. 46), and can be shown to be practically certain from a consideration of the phenomena which are connected with germinal duplicity and multiplicity, that is the production of more than one embryo from a single ovum. Amongst these phenomena we have (*a*) *on the purely teratological side*, the occurrence of double or multiple monstrosities in all classes of animals; (*b*) *intermediate between teratology and normal ontogeny*, the occasional production in the higher animals of complete and separate unioval twins or triplets; (*c*) *in normal ontogeny*, the polyembryony which occurs in the development of the edentate mammal *Tatusia* (p. 38) and the alternation of generations which has taken a definite place in the life-history of various groups of animals; (*d*) Lastly, *on the experimental side* and in illustration of what was said under II. above, it need hardly be pointed out that we have now numerous well-ascertained instances in which double or multiple forms have been artificially produced through the (virtual or complete) separation of individual cells or of cell masses during early stages in the development of a single ovum.

LITERATURE RELATING TO THE TERATOLOGY OF FISHES.

THE following index has been compiled from *Zoological Records*, *Jahresberichte*, and many other sources of a more general nature. Work on variation, experimental zoology, and regeneration has been included, only when it seemed to have a direct bearing on the main theme. It is hoped that the lists may not show greater defects than are pardonable in a first bibliography on a wide and scattered subject, and that they may fulfil the primary purpose of being useful to future workers. Throughout the succeeding parts of this Memoir, the papers, etc., to which reference is made, are cited under the authors' names and the list numbers, the latter in italic figures.

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CHAPTER I. DOUBLE MONSTROSITY.

(*For Contents see p. vii.*)

A. LITERATURE.

References will be found under the following index figures (pp. xi-xvii):

Salmonidae.—d'Audeville *4*; Barbieri *6-7*; Bugnion *34*; Coolidge *42*; Coste *43*; Dareste *52*; Garman and Denton *74*; Gemmill *76-77*; Girdwoyn *81*; Jacobi *108*; Klaussner *123*; Knoch *127*; Kopsch *132-133*; Lowne *146*; Moser *165*; Oellacher *175-176*; Panum *180*; Quatrefages *197-198*; Rauber *200-202*; Schmitt *216-7*; Schwalbe *222*, ii. p. 297 *et seq.*; Secques *224*; Sutton *245*; Taruffi *247*; Windle *271-2*; Yarrell *275*, ii. p. 107.

Other Fishes:—

Perca—v. Baer *5*; *Leuciscus*—Bataillon *11*; *Anarrichas*—Buckland *33a*; *Girardinus*—Emeljanov *65*; *Esox*—Klaussner *123*, Lereboullet *141-143*, Rauber *200*, Rauber *202*, Valentin *263*; *Blennius*—Rathke *199*; *Scomber*—Sutton *245*; *Selachoidei*—Aldrovandi *2*, v. Baer *5*, Gadeau de Kerville *73*, Heusner *94*, Klaussner *123*, p. 12, Levison *144*, Lowne *146*, Quatrefages *198*, Risso *205*, St. Hilaire *213*, Sutton *245*; *Torpedo*—Dohrn *57*; *Petromyzon*—Bataillon *12*. See also pp. 30-32.

B. OCCURRENCE, RECORDS, AND GENERAL OUTLINE.

From the scattered data available, it would seem that the frequency with which double monstrosity makes its appearance in the development of fishes varies in different species and in broods from different parents within the same species. The following figures apply to the Salmonidae: 1 in 50, and 1 in 280 (Rauber *200* and *202*); 1 in 600, none in 600, and 68 in 900 (Schmitt *216*); 1 in 200, and 1 in 350 (author's observation); over 100 in 400,000 (Coste *43*). Oellacher (*176*) notes a remarkable brood in which the proportion probably reached as high as fifty per cent., or at any rate twenty to thirty times more than the average. Here, however, the duplicity was of the peculiar and imperfect type described by this author as *mesodidymus*.

On the other hand, v. Baer (*5*) examined over 3000 eggs of *Cyprinus blicca* without result. In *Perca fluviatilis* he obtained two double embryos out of a set of forty eggs, although a very much larger number (over 1000) in other sets provided none. Lereboullet (*141-143*) examined in all 203,962 eggs of the pike (*Esox lucius*), obtaining 222 double monsters, an average of 1 in 920. In the same species Rauber (*202*) found a single example in a set of 325 eggs, and Valentin (*263*) six out of 917 hatched embryos. In *Petromyzon*, Bataillon (*12*) records an extraordinary case where forty out of a hundred eggs developed twin gastrulae. We owe to Lereboullet (*143*) the illuminating statement that within the same species (*Esox lucius*), the prevalent types of monstrosity as well as the frequency with which these occur vary somewhat in different groups of eggs. Much work, however, remains to be done on frequency and type in relation to parentage, alike on the male and on the female side, though some interesting figures bearing on the latter are given by Rauber (*202* **6**, 129-184).

It is worthy of note that the frequency with which double monstrosity appears in the eggs of fishes,

is not far from corresponding with its frequency in those of the fowl. Dareste's (*53*) figures showed out of 10,000 eggs, 38 examples of double and 2 of triple monstrosity, an average of 1 in 250.

Records of double monster fish do not seem to have come down to us from the ancients, and although the *Fish* has been employed in symbolism and mythology since earliest times, no shape it has received seems to indicate such acquaintance with its teratology as is undoubtedly implied for that of the higher animals in the Janus, Cerberus, Cyclops, and other fables. The reason is not far to seek. With the rarest possible exceptions, monster fish die off so soon as the store of food contained in the eggs on which they develop has been exhausted, and at this period they are still small in size and remote from ordinary observation.

The first notice of a double monster fish appears to be that contained in the *Monstrorum Historia* of Aldrovandi (*2*), a work brought out some thirty years after Aldrovandi's death by his loyal pupil Ambrosini. The notice bears out that a two-headed fish almost as large as a crocodile was caught in the Nile near the town of Latislana. The figure appended is that of a monster shark-like fish. No shark-like fish, however, seems to be the inhabitant of the Nile (Boulenger, *Brit. Mus. Cat.* "Fresh-water Fishes of Africa," i. 1909). Examples of double-headed shark or dog-fish *embryos* are not unknown (see under *Selachoidei*, above, and on p. 31), and in all probability some such specimen supplied the substratum of the record and story.

The only instances of survival or reputed survival of fish exhibiting a *major* type of monstrosity which I have been able to come across are the following: (1) The story in Aldrovandi given above; (2) Perfectly authentic accounts by Seeques (*224*) of a gasteropagous twin *Salmo lacustris* and of another similar twin *Salmo fario*. Both examples were about fifteen months old. In the first, one of the twins was larger than the other and measured about 6½ inches. In the second, the twins were of equal size, each being rather more than 5 inches in length. (3) A notice in Yarrel (*275*, ii. p. 107) from a Cambrian newspaper of 28th November, 1829, regarding the capture of a "fine Salmon with two heads and two tails. The heads are joined on one neck and the tails meet about the centre. The fish is now to be seen alive in a small pool at Llangattock." (5) Account of a cyclopic ray by Paolucci (*181*), referred to further on p. 43. F. Buckland (*33a*) also mentions that he "once read an account of a double-headed catfish (*Anarrichas lupus*) having been caught in the North Sea."

Jacobi (*108*) seems to have been the first not only to make systematic observations on the artificial breeding of trout, but also to note and describe the monstrosities which made their appearance in the broods, and to speculate on the causes of their occurrence. A translation of his highly interesting original letter on the subject will be found in Yarrell (*275*, ii. *87-96*). As teratology developed into an exact science in the hands of Meckel (*156*), St. Hilaire (*213*), v. Baer (*5*), Vrolik (*266*), and others, careful attention was paid to the study of monstrosities in fishes, particularly since their growth and development could be observed in the living condition with the aid of the microscope. It is probably to St. Hilaire's influence that we owe the studies of Valentin (*263*), Quatrefages (*197-8*), Coste (*43*), and Lereboullet (*141-3*), which followed each other closely towards the middle of last century. Lereboullet's work is particularly valuable, and still remains as containing standard results. Some of these have been already noted, while others are referred to under Causation (p. 5) and Structure (p. 10).

Later, the careful studies in normal embryology, of which His's observations on the development of the bony and cartilaginous fishes are an example, had their influence in stimulating renewed observations by means of the newer methods on the origin and structure of monstrosities in fishes (Oellacher *176*, Rauber *200-2*). Very useful work along descriptive, classificatory, and historical lines has also been done by Knoch (*127*), Panum (*180*), Rauber (*200-2*), Klaussner (*123*), and more lately by Windle (*272*) and Schmitt (*216*). The methods of experimental embryology, particularly in the hands of Kopsch (*129-133*) and Morgan (*161-2*), have supplied evidence of the greatest value in regard to the processes of normal and teratological development. On the structural side, our knowledge of detail has gradually been elaborated by the work of Rauber (*202*), Oellacher (*176*), Schmitt (*216*), Moser (*165*), Barbieri (*6-7*), and the author (*76-77*).

C. CLASSIFICATION.

In Teratology, the terms (1) *anadidymus*, (2) *katadidymus*, (3) *anakatadidymus*, and (4) *mesodidymus* are accepted as indicating respectively (1) doubling at the anterior end, (2) doubling at the posterior end, (3) doubling at both anterior and posterior ends, and (4) doubling in the middle region of the body. As regards fishes, it should be noted that the first (anadidymus) is much the most important; the third is practically confined to examples of union by the yolk-sac only; while the second and fourth, so far as seems to be known at present, do not provide examples of complete duplicity (p. 25).

We owe the first three terms (anadidymus, katadidymus, and anakatadidymus) to Forster (*Missbildungen des Menschen*, Jena, 1861, pp. 22, 29, 34), but it is to be noted that this author assigned to the first two of them a meaning exactly the converse of that in which they are now employed, having apparently applied the initial preposition to indicate the region of union instead of the region of separation. His anadidymus is thus the katadidymus of later authors. The fourth term, mesodidymus, we owe to Oellacher (*176*), but for reasons that will appear afterwards (p. 25) this term (as well as katadidymus) may with advantage be replaced by *hemididymus*, the substitute suggested by Rauber (*200* **79**) and adopted by Kopsch and others.

Of the groups above named, only the anadidymi, by reason of their number and variety, require detailed subdivision. The various schemes proposed need not be given here. Most authors dealing with the subject have adopted simpler or more elaborate methods of classification depending on the level at which union takes place. For external and descriptive purposes the scheme given by Windle (*272*) will be found convenient and inclusive. His classes are as follows:

1. Head union, three eyes present, all of the same size.
2. Do. three eyes present, the median one being larger than the others.
3. Do. four eyes present.
4. Two quite separate heads.
5. Fission extending to the pectoral region.
6. Duplicity extending to the posterior border of the yolk-sac, the caudal extremity being quite single.
7. Duplicity extending a short distance behind the posterior border of the yolk-sac, the caudal extremity being quite single.
8. Duplicity extending to the posterior border of the yolk-sac, the caudal extremity not, however, being perfectly single.
9. Union by the caudal extremities alone.
10. Union by the ventral aspects at the site of attachment of the yolk-sac.
11. Parasites, one member becoming an appendage to the other.

A less convenient, though logically sound system, is proposed by Schmitt (*216*), who would divide double monsters in fishes according to the manner in which they come together at the region of union. He thus distinguishes:

(1) Union by the yolk-sac only. (2) Simple ventral union. (3) Union principally ventral, but partly lateral. (4) Union half lateral and half ventral. (5) Union principally lateral, but partly ventral. (6) Simple lateral union. (7) Union so intimate that externally the duplicity is concealed.

The classification which will be adopted in this work is given below. It has reference alike to external features and to important points of internal structure.

Class I. Union in head region, the twin brains uniting at the optic lobes.[1]

Class II. Union in head region, the twin brains uniting at the medulla oblongata.

[1] Regarding the possible need for a Class to come in advance of my Class I., as showing a still less marked degree of anterior duplicity, see the second last paragraph under *Reduction and Parasitism* (p. 59).

Class III. Union in pectoral region, adjacent pectoral fins not being present.
Class IV. Union in pectoral region, adjacent pectoral fins being present, but united and reduced in size.
Class V. Union by the body or tail, the united portion ending as normally in a single symmetrical tail.
Class VI. Union by the body or tail, the united portion ending in a composite tail with various structures still doubled.
Class VII. Union by the yolk-sac only, or by the yolk-sac and the ventral edge membrane close behind it.
Class VIII. The condition of imperfect doubling exhibited by (*a*) the (hemi)mesodidymi and (*b*) (hemi)katadidymi (p. 25).
Class IX. Longitudinal or parallel union.

Comparing this scheme with the one given by Windle it will be seen that

Class	I.	corresponds (approximately)	with	1-2	of Windle.
,,	II.	,, ,,	,,	3	,,
,,	III.	,, ,,	,,	4	,,
,,	IV.	,, ,,	,,	5	,,
,,	V.	,, ,,	,,	6-7	,,
,,	VI.	,, ,,	,,	8-9	,,
,,	VII.	,, ,,	,,	10	,,
,,	VIII.	,, ,,	not represented.		
,,	IX.				

With regard to parasitic forms, though it may be convenient for descriptive purposes to group them together, as in Class 11 of Windle's scheme, they should more properly be distributed among the other classes according to the attachment of the parasite.

Schmitt's scheme and mine do not so readily fit into one another. From the practical point of view the former is chiefly useful in the analysis of the forms which are grouped under Classes V. and VI. of the latter (pp. 20-23).

It must be kept in mind that any scheme for the classification of *anadidymi* can only aim at dividing up into convenient groups a series of forms which is essentially continuous and unbroken, the members differing from one another by characters which depend mainly on the distance which separated the component twins at the time of their first appearance on the margin of the blastoderm. As will be explained under E (p. 6), these components are brought together during the natural elongation of their embryonic axes, and unite in what is designated *primary fusion*. On the other hand, it is probably as a result of the working of *secondary fusion* that such discontinuities as can be recognised in the series take their origin—for example, that twins united in the head region can always (so far as my experience goes) be grouped under Class I. or Class II., the final union of their brain cavities being fixed either in the region of the optic lobes or in that of the medulla. In the same way, though in a less striking degree, secondary fusion has helped to mould the structural details in the succeeding groups as well as to accentuate the external characters which have been employed above in their classification. Other references are made to secondary fusion on pp. 11, 15, 30, 43.

D. CAUSATION.

There is strong reason for believing that the occurrence of double monstrosity is due in the main not to environmental factors, but to conditions which are inherent in the fertilised germ cell. Lereboullet's (*143*) observations on the pike went to show that in spite of sameness of environment, different broods of eggs give rise to different prevailing types, as well as to different propor-

tionate numbers of monstrosities. So far as one can gather, this seems also in a general way to be the experience of fish hatcheries, though full and careful records from these are not as yet available. Von Baer's (*5*), Oellacher's (*176*), and Rauber's (*202*) observations point to the same conclusion, which may also help to explain the exceedingly wide variations in the other frequency records (p. 1). Lereboullet further notes that samples of the same brood of eggs tend to exhibit similar types and numbers of monstrosities even under differences of environment. Indeed, the only constant result which could be ascribed to the action of external factors was the production of defects in development. It will be noted that this corresponds on the whole with the data afforded by Dareste's (*53*) experiments on the eggs of birds. Evidence may also be adduced on the general question from a consideration of the relative frequencies of double and triple monsters (see note on p. 33).

The likelihood cannot, of course, be excluded, that external factors sometimes induce the production of double monstrosity in the developing eggs of fishes. As is well known, this has been done experimentally in the case of many invertebrate and of some vertebrate ova. The result has usually been obtained through virtual or complete separation of individual cells or of cell masses in the earlier segmentation stages. It will obviously be difficult to produce the requisite degree of separation in typical meroblastic ova, and particularly in those of the Salmonidae, where the earliest divisions affect the nuclei alone, and the first stages in segmentation are syncytial ones.[1] The above circumstances may help to explain the common failure of experiments on twin production in the eggs of osseous and cartilaginous[2] fishes as compared with the fruitful results of similar experiments in the Amphibia, and to some extent also in the lamprey (Bataillon *13*). This last author's (*14*) apparent success in producing polyembryony in the eggs of *Leuciscus*, through differences of osmotic pressure, should also be noted (see p. 30), but it does not by any means invalidate the view that the ordinary occurrence of duplicity in fishes is germinal rather than environmental in its origin. The same thing holds good regarding the occasional production of *katadidymus* under experimental conditions (Lereboullet *143*, Stockard *236*, Kopsch *132*). In fishes this condition provides an entirely peculiar type of duplicity (p. 25).

The production from a single ovum of twins or of twin embryos more or less united has long been known to occur from time to time in all classes of vertebrate animals. Recently polyembryony has been shown to be the normal condition for the edentate mammal *Tatusia*,[3] in which the seven or eight young produced at a birth all develop from a single egg.

The view has often been suggested that the blastoderm may be looked upon as a stock, able to give rise vegetatively, so to speak, to more than one embryo. The natural comparisons have been drawn between this faculty and the alternation of generations which occurs normally in some groups of lower animals and in plants. It has even been sought to recognise alternation of generations in the development of all animals. More probably, however, in animals, twinning, double and multiple monstrosity, polyembryony, and alternation of generations, provide instances in which a common "potentiality" has become realised, and beyond that are not necessarily connected by any nexus of a direct or phylogenetic character.

[1] Kopsch (F.) in *Arch. Mikr. Anat.* **78**, 1911 (618-659).

[2] Recently Eismond (*63a*) has given an interesting account of experiments on the eggs of *Raia clavata* and *Raia alba* during the early segmentation stages. He finds that separated portions of a blastoderm often show remarkable activity in reuniting to form a whole, which may then proceed to normal development. On the other hand, the separated portions may remain apart or even undergo further spontaneous division, and a number of embryonic rudiments may arise in the complex thus produced. The number of rudiments in one particular case was four. Two of these were found on one of the fragments; the other two occurred each on a single fragment, whilst two of the fragments provided none. Later, the clefts between the fragments disappeared completely, and the blastoderm, now single to all appearance, proceeded to extend over the yolk. Two of the rudiments were, to begin with, at an angular distance of about 55° from one another on the margin of the blastoderm. A day later these rudiments were found to have become closely approximated. They were, however, no longer normal in appearance, but seemed to be in process of degeneration, and accordingly it was judged best to fix and preserve the whole specimen at this stage.

[3] Fernandez (M.), "Beiträge zur Embryologie der Gürteltiere," *Morph. Jahrb.*, Leipzig, **39** (302-333).

E. DEVELOPMENT AND EARLY GROWTH.

It will be remembered that in the normal development of most fishes the segmentation of the egg is partial, and leads to the formation of a cap-like or disc-like blastoderm, the edge of which becomes thickened at one part and gives rise to the rudiment of the embryo. Gastrulation takes place here, a "primitive streak" being formed, in part at least, by apposition of adjacent portions of the blastodermic margin (Kopsch; see further on p. 27). According to the concrescence theory (associated particularly with the name of His), the body of the embryo is formed by the coming together of the thickened margins of the blastoderm during the process by which this layer gradually overgrows the yolk.

The concrescence theory in its original form is no longer tenable, but the fact still remains that the thickened margins of the blastoderm, close to the developing embryonic axis, are used up during the early growth of the embryo, not in producing the axial organs, but in contributing material for the formation of the muscle plates and the lateral and ventral body walls. This fact is of cardinal importance in connection with what follows. A second point of great importance is that, while the blastoderm rapidly extends and grows over the yolk, the extension sooner or later slackens markedly in the region of the blastopore.

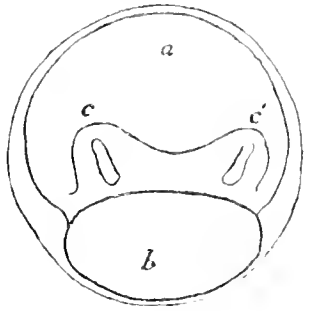

Fig. 1.

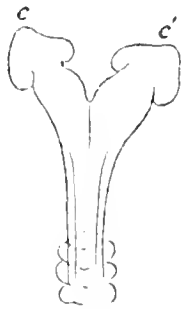

Fig. 2.

Fig. 1.—After Lereboullet (*143* 1863, Pl. III. fig. 14). Egg of the pike observed fifty-three hours after fertilisation. *a*, blastoderm spreading over the yolk; *b*, the portion of yolk not yet covered by the blastoderm; *c c'*, the two embryonic rudiments.

Fig. 2.—After Lereboullet (as above, fig. 15). Anterior part of the same double embryo observed twenty-six hours later (at commencement of fourth day). *c c'*, the two heads showing optic vesicles and uniting in the hind brain region. Further back is seen the commencement of the muscle somites.

The recorded observations indicate that double monster fishes always arise on a single yolk, and from a single blastoderm, at the margin of which two more or less separate centres of gastrulation (Hertwig *93a*) and embryo-formation have made their appearance. (We are leaving *mesodidymus* and *katadidymus* out of count till later (p. 25), because in fishes they constitute types of peculiar and imperfect duplicity. What is said on p. 28 regarding longitudinal or parallel union should also be borne in mind.)

The twin centres of embryo-formation mentioned above may be classed in two groups (*a*) and (*b*), according to the distance which separates them from one another. (*a*) In the first and most important group the interval is not too great to prevent approximation and union of the two embryonic axes from taking place during the natural course of their growth in length (see Text-figs. 1, 2 on this page). Approximation and union are due to the two factors to which attention was directed above, namely, the utilisation during growth of the blastodermic margins near the primitive streak, and the slowness of expansion on the part of the blastoderm over the yolk in this same region. The twin adjacent axes are inevitably brought together posteriorly through disappearance of the interval between them. The process may be called one of *primary fusion*, in contrast with a process which often supervenes later, and which consists in the *secondary fusion* of organs or structures already laid down.

Primary fusion takes place earlier or later, *i.e.* in the head-, body-, or tail-region, according to the interval which separated the embryonic rudiments when they first appeared. In other words, the degree of duplicity varies directly with the original distance between the two centres of embryo-formation. When the union is a purely lateral or an approximately lateral one, the posterior united part finally becomes simply and perfectly bilateral. This takes place through the gradual fusion and disappearance of structures belonging to the left and right halves respectively of the right and left component embryos. Thereafter the right and left halves of the right and left embryos unite naturally to form a normal bilateral body or tail. On the other hand, when the twin bodies come

together by ventral rather than by lateral union, the formation posteriorly of a perfectly single body or tail becomes impossible, since the necessary readjustments of right and left structures in the twin embryos can no longer take place.

(*b*) In the second group, the twin centres of embryo-formation are so far apart that there is no compelling influence of the kind described above which would lead to the approximation and union of their growing embryonic axes. Accordingly the twin bodies remain separate, except for the adventitious union supplied by the layers forming the wall of the common yolk-sac. Text-fig. 3 illustrates an early example in which the twin embryos are almost at opposite sides of the blastoderm. In the higher animals the corresponding type of doubling may give rise to completely separate unioval or homologous twins.

As is well known, in the higher animals well-developed unioval twins are always of the same sex, and they tend to show a remarkable degree of resemblance even in minute characteristics. In fishes, however, one of the twins is not infrequently smaller than its neighbour, or otherwise defective, no doubt through injury or want of room for growth. The defect sometimes takes the form of a pure cyclopia. Accordingly we have here a reason for believing that the natural occurrence of cyclopia need not be occasioned by conditions inherent in the fertilised egg, since otherwise both heads ought to be similarly affected.

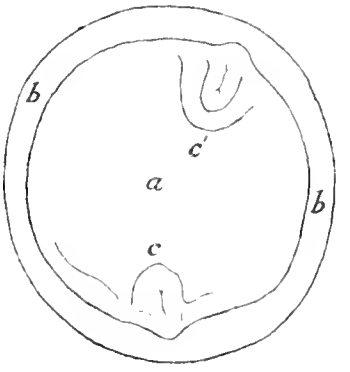

FIG. 3.—After Rauber (*202* 6, Taf. VIII, fig. 14). Egg of trout fourteen days after fertilisation, showing two embryonic rudiments, almost, but not quite, opposite to one another on the margin of the blastoderm. *a*, blastoderm spreading over the yolk; *b*, yolk uncovered by blastoderm; *c c'*, the twin embryonic rudiments.

There do not seem to be any direct observations enabling one to say what amount of angular distance must separate the twin embryonic rudiments on the egg of the trout in order that the twin bodies may remain apart from one another throughout their whole length. Taking it as a matter of chance at what part of the blastodermic rim each of the twin rudiments appears, one might seek evidence on the question by comparing the relative frequency with which union of the twin bodies and union by the yolk-sac only (*anakatadidymus*) are found to occur. Windle's figures (*272*) show two anakatadidymi out of a total of forty-six double forms. My own numbers are seven out of seventy-one. Summation of both gives an average of one in thirteen. Dividing the whole circle of the blastoderm (360°) by thirteen we get rather less than 30°. In the trout it would seem accordingly (if one assumes the correctness of the principle on which the calculation is founded) that, in order to remain axially separate, the twin embryonic rudiments must have appeared on the rim of the blastoderm not less than 165°, *i.e.* 180° − 15°, from one another. Probably this estimate of distance is too great. A larger number of instances to average from would likely reduce the figure, but Kopsch's (*132-3*) experiments seem to show that in any case it is over 90°.

All double monsters in fishes which are produced in the manner described above will be examples either of anterior duplicity or of union by the yolk-sac only. Further, in all cases the two heads will point in the same direction. Klaussner, however (*133*, Pl. V., Fig. 34), figures an example of union by the yolk-sac only, in which the twin heads are pointing in opposite directions, *i.e.* the head of the one lies alongside the tail of the other. This seems to be the solitary recorded instance of the kind, and Windle (*272*), in calling attention to it, notes that it is "difficult to account for by any of the theories now holding the field." Klaussner's figure is not a perfectly convincing one, but if correct could readily be explained by assuming the presence of two originally separate blastoderms on the parent egg. Such a condition, although it has never been observed in the eggs of fishes, is not unknown in those of other vertebrates. A number of instances are given below.

The foundation of our knowledge regarding the mode of growth and union of double monster fish embryos was laid by Lereboullet's work (*143*) on the living eggs of the pike (see p. 10). Very early stages (see pp. 9-10) have also been figured for the same species by Rauber (*200*), and for

the Salmonidae by Rauber (*202*), Kopsch (*132*) and Schmitt (*217*). Panum (*180*, p. 309) seems to have been the first to suggest in so many words that His's observations on normal development, which led up to the theory of concrescence, might be employed to explain the characteristic forms of double monster fish. On the experimental side we owe chiefly to Kopsch (*130*, *133*), Morgan (*161-2*) and Sumner (*242*) the crucial evidence that an embryonic body of full length and with the proper number of segments, but deficient in certain lateral and ventral structures, may develop after section or destruction of the thickened margin of the blastoderm to either side of the embryonic rudiment (see p. 27). The fact that the extension of the blastoderm over the yolk is delayed at, or near, the blastopore has long been known, and recently Kopsch's (*133*) experimental work has provided us with exact data as to the progress of this extension in the eggs of the Salmonidae.

Origin of double and multiple forms in vertebrates generally. Whatever be the causation, we may recognise, in vertebrates generally, four somewhat different *modes of origin*, whether for double (and multiple) monstrosities, or for double (and multiple) unioval separate embryos.

These different modes are: (1) The appearance of two (or more) embryonic rudiments on a single blastoderm (germinal area in the case of the mammalian blastocyst). (2) The presence in the egg of two (or more) separate blastoderms (germinal areas in mammalian blastocyst). (3) Fission or dichotomy on the part of a single embryonic rudiment. (4) Formation of certain axial structures in two parallel sets on a single embryonic rudiment.

(1) The first mode is universal in fishes, whilst in birds it holds good for the great majority of recorded instances. No doubt the same thing is true for reptiles. As regards mammals, direct observational evidence is awanting, but it is impossible to understand how the majority of double (or multiple) monstrosities can arise in any other way.

(2) The second mode is possibly illustrated in fishes by the unique example from Klaussner referred to above. It does not appear to be excessively rare in birds. Thus Dareste (*53*, Pl. I. fig. 4) figures two young blastoderms lying close together which have arisen from the development of two separate cicatriculae. In the succeeding figure the same author shows two blastoderms at a considerable distance from one another, each exhibiting traces of a degenerating embryo. Besides these, the first and fourth examples of triplicity in the chick quoted from Dareste (see p. 37 of this work) are marked by the presence of two separate blastoderms. But perhaps the best example in the chick is a seven days' embryo figured by Panum, which shows two well-developed embryos a considerable distance apart from one another, each surrounded by its own vascular area. Schwalbe reproduces this figure (*222*, II. p. 37), and on the same page he illustrates also a six-day incubated egg (described by C. W. Wolff) with two quite separate embryos on a single large vascular area. He also states on Panum's authority that Fabricius ab Aequapendente had observed two cicatriculae on the yolk of an unincubated egg. It should be added that Wolff's specimen only doubtfully indicates original doubling of the blastoderm.

In reptiles we have the *Tropidonotus* example figured by Wetzel (see p. 37 of this work), in which there are three centres of segmentation on the yolk, and one of the centres is itself double. Grandmann also has described an egg of *Lacerta* with a double blastoderm (quoted from Schwalbe, *222*, II. p. 29).

In mammals (see p. 38) the presence of more than one germinal area on the blastocyst is splendidly illustrated by the edentate *Tatusia* in which plurality is normal, while Assheton's observation shows that doubling of the germinal area can also occur in the blastocyst of the sheep, a mammal the development of which proceeds normally on more ordinary lines.

(3) The third mode accounts for certain examples of duplicity (chiefly posterior) in birds. There is every reason to believe that it occurs in a similar fashion among mammals as well, but the full discussion of this subject falls outside the scope of our work. In fishes the mode in question is represented only by the peculiar and imperfect doubling characteristic of the hemididymous condition (p. 25).

(4) The fourth mode is illustrated by the examples of longitudinal or parallel union which are referred to on p. 29.

A notice regarding the prevalence of the different types of double monstrosity in fishes and in other vertebrates is given at the end of the description of *hemididymi* (p. 28).

F. STRUCTURE.

Early Stages of Double Monstrosity in the *Salmonidae* and in *Esox* - - p. 9
Normal Advanced Embryos of *Salmo fario* - - - - - - - p. 11
Advanced Stages of Double Monstrosity in *Salmo fario*:
Class I. - - - - - p. 12
Class II. - - - - - p. 15
Class III. - - - - - p. 18
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Double Montrosity in other Fishes - - - - - - - - - p. 30

EARLY STAGES IN THE SALMONIDAE AND IN ESOX.

From the anatomical point of view, the stages of chief interest are those in which a large number of structures have become differentiated. Accordingly, the oldest available examples will be selected for detailed study. The anatomy of a normal trout embryo of corresponding age will also be described. But it may be well first to refer briefly to the earliest instances observed, beginning with the *Salmonidae*.

Rauber (*201*), in 1879, described an egg of *Salmo salar*, which is of normal size and has the blastoderm covering a small area at one pole. On opposite sides of the blastoderm two quite similar centres of embryo formation are appearing. Each shows a normal developing head rudiment. The bodies have not yet begun to form.

In the following year the same author (*202*) described seventeen Salmonid ova showing twin embryonic rudiments, and one showing a triple form. See Text-fig. 3 on p. 7, and Text-fig. 5 on p. 36. The whole provides an excellent series illustrating the different distances from one another at which twin embryos may appear, some pairs being exceedingly closely approximated, while others are at directly opposite sides of the blastoderm. Sections were also made by Rauber of several of these monstrosities.

Kopsch (*133* p. 233 Taf. XVII. fig. 21) figures and describes an extremely young stage in the trout. The centres of the two embryonic rudiments are separated from one another by an angular distance of something like 90°.

Schmitt (*217*) gives an account, with drawings, of two equally young stages in the same species. In the one case the centres are on exactly opposite sides of the blastoderm, while in the other they are almost so (155-165°). These two eggs would probably have given rise to twins with union by the yolk-sac alone.

The next earliest record for the *Salmonidae* seems to be that of Barbieri (*6*). It has reference to an egg of *Salmo irideus* fixed seven days after fertilisation, showing a double embryo 3 mm. long. This specimen is referred to further on p. 29.

Not much older than the above are two other instances of twin embryos recorded by Schmitt (*217*). They are at the stage when the blastoderm is just completing the overgrowth of the yolk, and they give valuable evidence that the process of overgrowth (as was indicated above) is delayed at, and near, the region where gastrulation began to take place.

The two specimens which Rauber (*200* **71**) examined by the method of serial sections have next to be mentioned. They are somewhat older than the foregoing. One is an example of union at the level of the optic lobes, and the other of union in the pectoral region. The figures given go some way

towards illustrating the behaviour of the more important organs (central nervous system, notochord, and Wolffian ducts) at the region of transition from the double to the single condition.

Of about the same age is the single specimen sectioned and described by Moser (*165*). The two central canals of the spinal cords unite near the fourth body somite, but the notochords only come together at the level of the vent. Inner or adjacent auditory organs are present, but reduced in size, and enclosed within the same cartilaginous capsule. The pronephros is peculiar, having three much reduced pronephric chambers and no proper glomerular tuft. It gives origin to three Wolffian ducts. Moser's paper also contains a discussion regarding the origin of double monstrosity in the light of recent experimental work bearing on the question of concrescence.

Still later stages are dealt with by Schmitt (*216*), and by the author (*76-77*). In the specimens which they describe, practically all the organs and structures found in the adult, except the osseous skeletal parts, have already made their appearance. Schmitt's work covers only union by the tail and extreme posterior part of the body, and will be referred to later in connection with the anatomy of these types.

Esox. The eggs of the pike equally with those of the trout and salmon have provided classical material for the study of double monstrosities. The first account of the growth from day to day of a developing double fish was given by Valentin (*263*) from observations on an example which he watched from the fifth to the thirteenth day. To Lereboullet's work on the same species we owe the fullest investigation which has yet been made regarding the occurrence, and mode of growth, of double monsters in any species. Out of a total of over two hundred thousand eggs examined, he obtained rather more than two hundred double monsters, very many of which he not only observed at an extremely early stage, but also followed in development till their final form became established. A seventy-two hours' stage in the pike was also figured and described by Rauber (*202* **6** Taf. IX. fig. 23), while two exceedingly early examples are illustrated by Klaussner (*123* Taf. I, figs. 1, 2).

Lereboullet (*143* **20** 254 *et seq.*) classified the different sequences observed by him in the growth of anomalous forms into the following six types:

1. Instances in which there are, to begin with, two separate embryonic rudiments. These tend to unite posteriorly, the resulting forms having either separate heads and bodies, or separate heads with united bodies.

2. Instances in which there is one broad embryonic rudiment showing more or less extensive doubling of the anterior axial structures. Later, by fusion and disappearance of inner elements, evidence of duplicity may disappear almost completely. Or one of the sets of structures may become atrophic.

3. One instance of a triple monstrosity. There are two bodies, one of which carries a pair of closely joined heads. An even younger triple Salmonid specimen has been described by Rauber (see p. 36).

4. Instances of the type afterwards called *mesodidymus* by Oellacher (*176*), in which the head and tail are single but the body is double. Each component tends to be defective as regards its inner or adjacent elements (p. 26).

5. Instances of thinness and slenderness of the embryonic rudiment followed later by defective formation of various organs, notably of the brain and organs of sense.

6. Instances in which no proper embryonic rudiment is formed at all. The blastoderm, however, succeeds in covering the yolk mass, and then a small tubercle makes its appearance, which represents the tail of the fish.

In his explanation of types 4 and 6, Lereboullet comes very near to enunciating a definite theory of concrescence.

Lereboullet's youngest example dated back to fifty-three hours after fertilisation, and showed two embryonic rudiments very close to one another, and united together at their posterior ends. A medullary groove was present in each. His next earliest observation had reference to an egg fifty-four hours after fertilisation. Here he described the embryonic rudiment as being single but broader than normal, and showing two parallel medullary grooves separated slightly from one

another in front. Two heads were thus formed, but in later development one of them remained as a rudiment, forming a knob attached to the other and containing traces of an eye.

Nothing is more striking in these and other observations by Lereboullet, than the amount of what may be called *secondary fusion* which can take place between closely approximated twin sets of structures, provided that they come together at a sufficiently early stage. For example, two head rudiments may, in the end, be converted into a single apparently normal head devoid of inner eyes or olfactory pits. Even two inner series of composite mesoblastic somites may unite, become absorbed, and disappear. Doubling of the notochord, however, seems never to be recalled, though the twin notochords may come to lie close against one another through absorption of the intervening tissue. The period when the power of fusion becomes lost in the case of mesoblastic somites is near the time of appearance of the heart.

ANATOMY OF NORMAL TROUT EMBRYOS.[1]

Pl. I. fig. 1 (external appearance); III. figs. 13-16, IV. figs. 17-20, VI. figs. 24-26 (transverse sections); V. figs. 21-23 (horizontal sections); diagrams of skeleton, heart, etc., in Pl. XVII. figs. 56, 57, 62, XVIII. fig. 69, XIX. figs. 73, 76, XX. fig. 83.

In normal trout embryos of the same age as the monstrosities, the cartilaginous skeleton has long been laid down and the process of ossification is about to commence.

Cranial Skeleton. The parachordal cartilages are uniting round the anterior part of the notochord and have already joined with the trabeculae cranii, which, coalescing in front of the pituitary space, run forwards as a median flattened bar to meet the nasal cartilages. The pituitary space gives passage to the choroidal and internal carotid arteries and to the back part of each rectus oculi externus. On either side, the parachordals have grown upwards in the form of laminar plates, which meet in the mid-dorsal line over the upper part of the medulla, but leave a narrow V-shaped fontanelle over the lower part. The auditory capsules are firm bosses of cartilage, moulded on the labyrinth, closed externally, but widely open towards the brain. Dorsally, they are connected with each other by a thin vault of cartilage roofing the cerebellum; anteriorly, they are continuous with the supraorbital bars to be afterwards described; ventrally, they join the trabecular and parachordal cartilages; and externally they articulate with the hyomandibulars. The 5th nerves emerge through deep grooves between the trabeculae and the auditory capsules, while the vagus and glosso-pharyngeal nerves pass out together through a foramen in the cartilage connecting the auditory capsules with the parachordals. A single opening in the floor of the capsules on either side gives passage to the internal jugular vein and the facial nerve. The nasal cartilage is connected with three pairs of bars: (1) the trabeculae cranii, (2) the palato-quadrates, and (3) the supraorbitals. These last pass backwards along the dorso-lateral angles of the brain to join the anterior part of the auditory capsules on either side. Over the pineal body and the third ventricle the supraorbitals are connected together by a bridge of cartilage, but no such *tegmen* exists over the cerebral and the optic lobes, the spaces left uncovered being the anterior and the middle fontanelles.

Visceral Arch Skeleton. The hyomandibulars are connected with (1) the outer aspect of the auditory capsules, (2) the posterior ends of the palato-quadrates, and (3) the interhyals. The Meckelian bars are slender, and meet below the mouth in a symphysis. Posteriorly they articulate with the palato-quadrates, but not with the hyomandibular or interhyal cartilages. In the hyoid arches, glossohyals, hypohyals, ceratohyals, and interhyals can be distinguished. The branchial cartilages are five in number, and have the usual forms and relations.

Pectoral Girdle, Notochord, etc. The pectoral girdle is represented by a comparatively short bar of cartilage on either side—the coraco-scapular—and is far from being a complete arch ventrally. The limb-cartilage is an unsegmented plate continuous with the coraco-scapular bar. The notochord consists of pith-like tissue surrounded by a very firm capsule, and its anterior end is embedded in

[1] Full references are given in the *Index of Structures, etc.* (p. 63) to the various Plates and figures in which individua structures receive illustration.

the fused parachordal cartilages. Its posterior end still shows a rapidly narrowing upturned "heterocercal" portion. In the position of each future vertebra there are four cartilaginous nodules, placed respectively at the dorso-lateral and ventro-lateral corners of the notochord, and prolonged into processes for the neural and haemal arches.

Nervous System, Heart, etc. The anatomy of the central nervous system and of the organs of special sense, and of the heart and blood-vessels, is, with certain differences in the relative size of parts, practically the same as in the adult condition. With regard to the aortic roots, it may be stated that the first root, *i.e.* the first branchial vein, gives off the hyoid and carotid arteries and then passes backwards to join the second root. The resulting trunk bends inwards to the middle line, and, meeting with its fellow from the opposite side, forms the upper part of the aorta. This part is next joined on either side by a trunk formed by union of the third and fourth roots. The carotids pass forward beneath the parachordals and, traversing the pituitary space from below, reach the base of the brain. The hyoid artery arises from the first aortic root at its ventral end, perforates the hypohyal, runs up along the hyoid bar, and, after passing through a foramen in the hyomandibular, is continued mainly into the pseudobranch. The efferent vessel of the pseudobranch passes forwards and inwards, traverses the pituitary space from below, and, after running alongside the optic nerve, ends in the choroidal gland of the eye. Of the two posterior cardinal veins, the left is usually the larger.

Kidneys. The head-kidney, or pronephros, contains a single median glomerular tuft of considerable size, supplied by a branch directly from the aorta. The Wolffian ducts begin by a funnel-shaped opening from the glomerular cavity on either side. Then, bending forwards, they become convoluted, and are embedded in highly vascular lymphoid tissue. They next arch backwards, remaining convoluted for a short distance, and end in a small urinary bladder. The mesonephros is just beginning to develop in connection with their middle and posterior parts. The urinary bladder opens by a mesial pore situated just behind the vent.

The intestinal canal is completely shut off from the yolk-mass, and there is an open diverticulum for the air-bladder.

Body Segments. The total number of body segments is approximately sixty, the vent being at, or near, the 36th segment. The posterior edge of the dorsal fin reaches to the 9th or 10th segment in front of the vent, and the anterior border of the adipose fin to the 7th segment behind that opening.

Median Fins. The median fins characteristic of the adult, viz. dorsal, adipose, caudal, and anal, are already well defined. These are still connected, by a low membranous ridge, which is best marked between the caudal fin on the one hand, and the adipose and anal fins on the other. A similar ridge is found between the anal fin and the vent, and also in front of the vent to near the level of the pelvic fins. In tracing the continuity of the mid-dorsal and mid-ventral lines along the transitional region in double monstrosities, it will occasionally be preferable to speak simply of dorsal and ventral edge membranes rather than to specify the particular fins.

ANATOMY OF DOUBLE MONSTROSITIES.[1]

CLASS I.

Union in Head Region, the Twin Brains uniting at the Optic Lobes.

Pl. I. figs. 4, 5 (external appearance); Pls. VIII.-IX. figs. 35-38 (transverse sections); Pls. X.-XII. figs. 39-46 (horizontal sections); diagrams of skeleton, vessels, etc., in Pl. XVII. figs. 58, 59, XVIII. figs. 64, 67, 70, 72, XX. figs. 84, 85.

In this Class, the region of transition from the double to the single condition involves the brain, the cranial nerves, and the organs of special sense, as well as the cranial, mandibular, and branchial cartilages. The twin heads are placed symmetrically, side by side, and lie in the same horizontal plane. Union is thus of the simple lateral type.

[1] See note at foot of p. 11.

Cranial Skeleton. There are two notochords in front, and therefore, potentially at least, two pairs of parachordal cartilages, but the four cartilages are united to form a single basilar plate. In front, the two nasal cartilages are placed widely apart; each contains a right and left olfactory pit, and is continuous behind with its own trabeculae cranii. The two pairs of trabeculae converge as they pass backwards; their inner [1] or adjacent elements unite to form a median flattened bar, which joins the basilar plate mentioned above as being formed by the parachordals. At the same time, the outer elements of each pair of trabeculae have diverged from the inner elements to enclose a pair of pituitary spaces, the latter lying one on each side of the median bar formed by union of the inner trabecular elements. There are only two auditory organs, and their cartilages are continuous with the outer trabecular and parachordal elements in the floor of the skull. Dorsally, the auditory capsules are connected over the cerebellum by a vault of cartilage, which is narrower antero-posteriorly than in the normal condition. Over the medulla the laminae of the parachordals nowhere form a complete vault. Accordingly, the posterior fontanelle is much larger than in a normal case. Dorsally, each nasal capsule is continuous with a pair of supraorbital bars, of which the outer elements pass backwards on either side to join the auditory capsules, while the inner or adjacent elements are connected with each other and with the outer bars over the pineal body. Behind this the adjacent bars disappear, the result being that over the region of the cerebral lobes there are two small anterior fontanelles, while over the optic lobes there is a single large fontanelle.

Visceral Arch Skeleton. The inner or adjacent palato-quadrate bars converge, fuse, and end abruptly without being attached to a suspensorium; the outer bars are continued backwards on either side, and articulate with the hyomandibulars attached to the auditory capsules. Articulating with the united part of the inner palato-quadrate bars is a small twisted piece of cartilage, which passes downwards in the septum between the two mouth-openings, and represents an inner or adjacent pair of Meckelian cartilages. The corresponding outer Meckelian cartilages meet in the septum between the two mouth-openings, but do not form a symphysis. They are continued backwards to articulate each with a normal suspensorium attached to the outer side of the corresponding periotic capsule. The hyoid bars and the branchial cartilages are normal, except that they diverge rather more widely than is usual. Each arch, however, may be looked upon as being composite, namely, as consisting of the outer components of a double set of arches, the inner components having been lost.

Notochords, etc. Two notochords are present as far back as from the 14th to the 20th body-segment. These converge at an acute angle and finally unite. The disposition of the neural and haemal arch cartilages is as follows. Where the two notochords are some little distance apart, the inner or adjacent neural arches are displaced so as to form a floor for the transversely-expanded spinal cord, while the inner haemal arches lose their ventral processes and become smaller. As the notochords come closer together and unite, the inner neural and haemal arches disappear, while the outer arches gradually assume a normal form and position.

Brain and Cranial Nerves. There are two pairs of cerebral lobes and two thalamencephala, diverging forwards from a single composite optic lobe region. The cerebral lobes and thalamencephala, besides diverging, are rotated slightly in such a way that they lie closer together dorsally than ventrally. There are two pairs of olfactory nerves, two pairs of optic nerves, and two pineal diverticula. There are also two infundibula, which converge as they pass downwards and backwards. Each ends in a hypophysis sac after giving off the usual diverticula for the hypoaria. The inner hypoarium on either side, owing to want of space, is smaller than normal, and lies above and in front of the outer hypoarium. The optic lobes show a remarkable transition between the double and the single condition. Their cavity and roof-parts are single, while the basal structures are doubled. There are thus two pairs of 3rd nerves. But only a single pair of trigeminals is found, the components of which represent, respectively, the right and left 5th nerves of the right

[1] In examples of lateral union like the present one, the terms *inner* or *adjacent* refer to those structures which gradually become approximated as the twins converge. Here, accordingly, the left trabecula of the right twin head and the right trabecula of the left twin head constitute the inner or adjacent elements in question.

and left twin heads. The succeeding cranial nerves are also normal, in the sense that there is only a single pair of each. A rudiment of inner or adjacent pairs of trigeminal ganglia may be recognised in the form of a thin elongated band of tissue containing small nerve-cells and lying in the middle line underneath the region of the pons. This band of tissue has no central or peripheral nerve-fibres. The pons and cerebellum are single, but their internal structure shows traces of duplicity, especially in the case of the pons. The medulla oblongata is slightly expanded transversely, but is otherwise normal in form.

Spinal Cord. In the anterior part of the spinal cord there is a curious and interesting reappearance of duplicity, coextensive with the duplicity of the notochords, and with the presence, ventral to them, of a median composite muscular mass representing united adjacent lateral muscles. In this region, the spinal cord is greatly expanded in a transverse direction; its cavity is spindle-shaped, and, in addition to the usual nerve-roots, it gives off, on the ventral aspect in each segment, a pair of small additional motor roots which are distributed to the median muscular mass just mentioned.

Organs of Sense. There are two pairs of olfactory organs and nerves. The outer eyes (right eye of right twin head and left of left head) are normal, but lie further back than usual, so that their optic nerves pass backwards as well as outwards from brain to eyeball. The inner or adjacent eyes may, or may not, be fused with one another. In the former case (which is also much the commoner) there is a single lens, which is sometimes smaller than normal, but sometimes larger and showing evidence of duplicity; the sclerotic and choroid coats are single; the retinae never fully unite, each showing its own choroidal fissure, optic nerve, and choroidal gland. In all cases the external recti muscles belonging to the inner eyes are absent; the superior obliques are absent or rudimentary, but the remaining ocular muscles are present in two sets.

Heart and Vessels. The heart and the ventral aorta are normal, but the dorsal aorta and its roots, as well as the choroidal and carotid arteries, require description. The coming together of the main collecting-trunks on either side to form the dorsal aorta is carried backwards for a very considerable distance, and takes place only at the level of union of the notochords. The pseudobranch on either side receives a branch from the hyoid artery, and its efferent vessel passes to the choroidal gland of the corresponding (*i.e.* outer) eye. The choroidal glands of the inner or adjacent eyes are supplied by blood which has not passed through the pseudobranch. In the specimen from which Pl. VIII. fig. 35 is taken, the arrangement of vessels is quite symmetrical and is indicated in Pl. XVIII. fig. 67. A transverse arch vessel connects the upper aortic roots, and gives off a common choroidal artery which soon bifurcates. The two resulting vessels pass through the separate pituitary spaces, and are distributed to the choroidal glands of the adjacent eyes.

As is well known through the work mainly of Johannes Müller,[1] the pseudobranch and the choroidal gland are so related to one another in osseous fishes that a pseudobranch is never present in species which have no choroidal gland, while in rare instances only is a choroidal gland present where there is no pseudobranch. It is therefore of considerable interest to note that the choroidal glands of the inner or adjacent eyes, in the type of monstrosity under consideration, derive their blood-supply directly from the first aortic root. There is a certain amount of variation in the exact mode of origin of the choroidal and carotid arteries. For instance, cases occurred in which these vessels all arose from the first aortic root on one side only, instead of both roots participating equally as in the specimen figured (Pl. XVIII. fig. 67).

Kidneys, etc. The mesonephros, ureters, bladder, and urinary pore are normal, but the pronephric glomerulus is composite, or may be double. An example of the composite condition is figured in Pl. XIX. fig. 84. The glomerulus is larger than normal, and contains two vascular tufts between which is a median compartment that obviously corresponds to the fused adjacent halves of a pair of glomeruli, but has no Wolffian ducts in connection with it. In the specimen from which Fig. 85 is taken the two glomeruli are separate, and one of them has a rudimentary Wolffian duct arising from its inner side, while the other has none at all. The two figures should be com-

[1] *Vergleichende Anatomie der Myxinoiden*, Berlin 1835-1845; 3te Fortsetz. 1841 (41-99).

pared with Figs. 86 and 87 on the same Plate, which show a still greater degree of duplicity in the pronephros.

Alimentary Canal. There are two mouth-openings, but the pharynx and the rest of the canal are single, the only evidence of duplicity being the presence of two air-bladder diverticula.

Muscles. Of composite muscles, the most important are contained in the median mass mentioned above as underlying the twin notochords, and as being innervated by the small additional motor roots of the composite spinal cord. This muscular mass is segmented serially by septa which correspond exactly with the septa of the outer (normal) lateral muscles. In the head-region some small and intricately arranged muscles are found connected with the cartilages which represent the reduced adjacent Meckelian and palato-quadrate bars. These muscles are obviously rudiments of adjacent mandibular and temporal muscles. It has been noted previously, that there are no external recti muscles in connection with the adjacent eyes, and that the superior obliques are either rudimentary or entirely absent.

Summary for Class I. Union of simple lateral type (p. 6), the twin brains uniting at the optic lobes; notochords wider apart in the cervical than in the cranial region, and uniting between the 14th and the 20th segments; body thereafter having a normal bilateral structure; skeletal elements in floor of cranium doubled from pituitary region forwards; doubling less marked in roof of cranium, and practically absent in visceral arch skeleton; greater doubling in the floor than in the roof of the brain, and in the first part of the spinal cord than in the medulla; four separate olfactory pits; inner eyes more or less united; inner auditory organs not represented; heart normal; vessels slightly modified; pronephros much modified; gut single, but with two air-bladder diverticula. The chief uniting and composite structures noted are: the trabecular, parachordal, palato-quadrate, Meckelian, supraorbital, neural, and haemal arch cartilages; the eyes; the central nervous system from mid-brain to upper end of spinal cord; the inner muscle plates, and the pronephric glomerulus.

Secondary Fusion. The part played by *primary fusion* in the very early growth of double monster fish was previously described (p. 6). It was stated also that *secondary fusion* had to do with the union of tissues already laid down and the attempted production of a more or less normal bilateral condition out of a double set of structures. In Class I., which has just been described, we may trace the working of secondary fusion in the following, among other, characteristics: (1) the practically normal condition of the visceral arch skeleton; (2) the fact that the roof parts of the cranial skeleton, optic lobes, medulla, and first portion of spinal cord are less modified than the corresponding floor parts; (3) the fact that the first portion of the spinal cord shows greater duplicity than the medulla; (4) the single condition of the pharynx, oesophagus, and heart, as contrasted with the doubling of the air-ducts; (5) the delayed union of the dorsal aortae, and (6) the double or composite character of the pronephric glomerulus.

Influence of Sensory Nerves on Growth. Important evidence on this vexed question is afforded by the monstrosities just described. No trace exists of inner or adjacent 5th and 7th cranial nerves. Yet the inner sides of both heads are perfectly well developed wherever they have sufficient space for growth. It is thus evident that, here, the absence of a sensory nerve-supply has neither hindered nor disturbed the natural course of development.

CLASS II.

Union in Head Region, the Twin Brains uniting at the Medulla Oblongata.[1]

Pl. I. fig. 6 (external appearance); Pls. XIII.-XIV. figs. 47-51 (transverse sections); diagrams of skeleton, vessels, etc., in Pl. XVII. figs. 60, 61, XVIII. figs. 65, 68, 71, XX. figs. 82, 86.

Cranial Skeleton. The structure of the cranial skeleton in this type agrees generally with that in the class last described, except that the place of union of the skeletal elements is carried further back. This gives room for greater development on the part of the inner or adjacent elements in the

[1] See note at foot of p. 11.

twin heads, but the union is again of the simple lateral type. The two pairs of trabeculae converge posteriorly, but are separate along their whole length, and unite with corresponding parachordals. The latter are separate in front, but posteriorly the adjacent elements in each pair unite, so that a single composite basilar plate of cartilage containing two notochords underlies the posterior half of the medulla oblongata. The inner or adjacent palato-quadrates converge posteriorly and coalesce. The united part articulates, (1) below, with a small bifid cartilage representing fused adjacent Meckelian bars; and (2) higher up, with a small cartilage representing fused adjacent hyomandibulars. The inner or adjacent supraorbital bars converge posteriorly, unite with one another, and end by becoming continuous with the roof of a small box of cartilage, wedged into the apex of the angle between the twin heads, and representing fused adjacent periotic capsules. This structure will be described later, but it may be mentioned here that its roof is continuous posteriorly with a vault of cartilage which connects the two outer (normal) periotic capsules over the cerebella. In this way double sets of anterior and middle fontanelles are left over the cerebral lobes and mid-brains respectively of the twin heads.

The inner or adjacent auditory capsular cartilages are extremely rudimentary, being completely united, compressed from side to side, and wedged into the position above indicated. They contain a single distorted labyrinth, and receive small auditory nerves on either side, which are distributed symmetrically over the labyrinth. This composite auditory capsule is connected anteriorly with the fused adjacent supraorbital bars, and ventrally with the adjacent trabecular and parachordal cartilages on the inner sides of the two pituitary spaces. Behind it a small triangular opening is left, bounded on either side by the converging parachordals. These unite posteriorly, but leave a narrow foramen between them for the exit of a small nerve, which represents a reduced adjacent pair of vagus and glosso-pharyngeal nerves. It will be seen from what precedes, that there are five fontanelles, one over each pair of cerebral lobes, one over each mid-brain, and one over the composite medulla oblongata.

Mouth. There are two mouth-openings placed side by side, separated from one another by a thick dorso-ventral septum. This septum contains (1) remains of the adjacent mandibular and hyoid cartilages, (2) much confused muscular tissue, and (3) two arteries which will be afterwards described, one being a continuation of the ventral aorta, and the other a small artery for the supply of the inner or adjacent pseudobranchs. The two mouth-openings lead into separate buccal cavities, but the oesophagus is single, the septum above mentioned ending opposite the second branchial cartilage.

Visceral Arch Skeleton. The inner or adjacent hyomandibulars are extremely rudimentary, and are fused together to form a small bifid piece, which articulates (1) anteriorly, with the fused adjacent palato-quadrates, (2) posteriorly, with the fused adjacent periotic capsules, and (3) inferiorly, with a rudiment of the fused adjacent hyoid bars. The small artery for the supply of the inner or adjacent pseudobranchs passes up through the notch at the anterior end of this cartilage.

The mandibular apparatus may be described as consisting of a composite arcade underlying the two mouth-openings. The outer portions of this arcade are formed by normal (outer) Meckelian bars (*i.e.* right bar of right twin head and left bar of left head), while a small mesial portion of the arch is formed by rudimentary adjacent Meckelian bars. These latter bars are united at their proximal ends, and there articulate with the fused adjacent palato-quadrates. Distally, each of the inner bars unites in a symphysis with its corresponding outer Meckelian bar. As the inner bars are extremely reduced in size, the two symphyses lie close together in the tissue of the septum separating the two mouth-openings. The hyoid apparatus may also be described as forming a composite arcade, the main part of which consists of the outer arches of the twin heads, while in the middle are interposed the fused remains of the inner arches.

These remains consist of (1) a single twisted piece of cartilage articulating, without the intervention of an interhyal, with the fused adjacent hyomandibulars, and representing ceratohyals; and (2) two incompletely separated hypohyals, articulating below with two glossohyals which are also incompletely separated. Connected with the outer sides of these glossohyals are the

hypohyal pieces of the outer arches. No adjacent elements are interposed in the series of branchial cartilages. Here, the only evidence indicating duplicity is to be found in the second copular piece, *i.e.* that succeeding the glossohyals. This piece is double anteriorly, but it becomes single opposite its articulation with the second branchial cartilages. The succeeding copular pieces are single, but they are a little broader than normal, especially in front.

Notochords, etc. The notochords remain separate as far back as the twentieth to the twenty-eighth somite. The arrangement of the neural and haemal arch cartilages in the transition region is the same as that described on p. 13.

Brain and Spinal Cord. There are two sets of brain cavities and masses as far back as the level of the fourth ventricle. The fourth ventricle is single posteriorly, but it bifurcates in front into two canals leading into the separate mid-brains. The posterior part of the medulla and the anterior part of the spinal cord are composite, and show the following characters: (1) they are much drawn out transversely, and (2) they give origin to small inner nerve-roots. In the medulla these roots are extremely rudimentary, and their ultimate distribution could not be traced, but in the spinal cord they are better developed and form a regular series of pairs of nerves coming off from the ventral aspect of the cord and distributed to the somites of the median muscular mass which lies ventral to the notochords (compare p. 15). In this monstrosity, as in the one previously described, the anterior part of the spinal cord, though it lies nearer to the place of union of the twin bodies, shows greater structural duplicity than does the medulla oblongata.

All the outer cranial nerves belonging to the twin heads are normal, and need no further mention. Of the inner or adjacent nerves, the 1st, 2nd, 3rd, and 4th are normal, while the 5th are reduced in size. The inner or adjacent 7th and 8th nerves with their ganglia are very rudimentary; while only a remnant of the adjacent glosso-pharyngeal and vagus remains. I was unable to follow out the 6th pair, but the presence of well-developed external recti muscles makes it probable that these nerves are present.

Auditory Organs. As has already been mentioned, the inner or adjacent auditory capsules are much reduced in size, their auditory sacs being completely united and forming a single labyrinth, symmetrical in shape, compressed from side to side, and receiving the two adjacent auditory nerves. The arrangement of the sensory epithelium inside the various parts of this labyrinth is also bilaterally symmetrical. A diagram of this labyrinth is given in Pl. XX. fig. 82. Utricle, anterior, and posterior semicircular canals are all represented, but there is no trace of a horizontal semicircular canal.

Heart and Vessels. The heart is normal and gives origin to a single ventral aorta, which, for a short distance upwards, has a double cavity, owing to the presence of a median antero-posterior septum, which, however, disappears further forwards. The gill-arteries on either side are normal, but, in addition to them, the ventral aorta gives rise to several small irregular branches which ramify in spongy tissue surrounding the ventral ends of the branchial cartilages, and may be taken to represent a very rudimentary set of inner or adjacent gill-arteries. But the most striking feature of the ventral aorta is that, instead of ending in the first gill-arteries, it is continued forwards and arches dorsally in the tissue of the septum between the two mouth-openings. Passing through the space between the adjacent glossohyals and the succeeding copular piece, it comes to lie behind the small cartilage which represents adjacent ceratohyals. Then, reaching the base of the skull, it bends backwards, and divides into two equal branches which join the upper aortic roots on either side. In the first part of its course, this continuation of the ventral aorta gives off (1) two inner or adjacent carotid arteries, which, after running forwards and outwards, pass through their corresponding pituitary spaces; and (2) two arteries for the supply of the inner or adjacent pseudobranchs. These arteries run at first forwards and dorsalwards behind the adjacent glossohyals. They next curve forwards and unite in front of the adjacent ceratohyals; then, separating again, they pass between the adjacent palato-quadrates and the hyomandibulars, and are distributed each to its corresponding pseudobranch. On either side the first aortic root gives off (1) a hyoid artery which sends a branch to the corresponding outer pseudobranch, and (2) a carotid artery. It then joins the second aortic root, and shortly afterwards meets the continuation of the ventral aorta previously mentioned. The

resulting vessel is next joined by the third and fourth aortic roots, but it remains separate from its fellow on the other side, so long as the notochords are separate, *i.e.* back to the twentieth somite.

The arrangement of vessels which has just been described and is illustrated in Pl. XVIII. fig. 68, is somewhat remarkable. Mixing of arterial with venous blood must have taken place in no slight degree, and certain parts in each twin head must have been supplied by blood coming directly from the ventral aorta. There is no trace of a pair of adjacent jugular veins, and it is difficult to make out from sections the course of the venous blood coming from the adjacent sides of the twin heads. But as there is a considerable amount of spongy tissue below the base of the skull and in the septum between the mouth-openings, it is probable that the blood in question found its way into the median and the main jugulars. The presence of this spongy tissue no doubt indicates congestion.

Kidneys. The pronephric glomerulus is composite. It is remarkably large, and is divided into three compartments by two vascular tufts each of which has an afferent and an efferent vessel. Normal Wolffian ducts arise from the outer compartments, while the middle compartment gives origin to a sacculated tubule which passes backwards a short distance to end blindly, and represents fused adjacent Wolffian ducts.

Alimentary Canal. There are two buccal cavities, but the oesophagus and the rest of the alimentary tract are single except for the presence of two air-bladder diverticula.

Summary for Class II. Union of the simple lateral type occurring at the hind-brain; notochords further apart in the cervical than in the cranial region, and uniting from the 20th to the 30th body-segment; body thereafter having a normal bilateral structure; skeletal elements in floor of cranium doubled from parachordal region forwards; very little doubling in the visceral arch skeleton; greater duplicity in the floor than in the roof of the medulla and first portion of the spinal cord; all four eyes separate; inner auditory organs present but reduced; heart normal; vessels and pronephros greatly modified; mouth partly double but pharynx and gut single; two air-bladder diverticula.

The chief uniting and composite structures noted are: the parachordal, palato-quadrate, Meckelian, hyoid, supraorbital, auditory, neural, and haemal arch cartilages; the medulla and first part of the spinal cord; the ventral aorta and various large vessels; inner muscle plates; pronephros.

That secondary fusion has played an important part in the ultimate moulding of the transitional region in this type is evidenced by a set of characters almost exactly comparable with those referred to in the description of Class I. (p. 15). What is said on p. 4 and p. 11 should also be referred to in this connection.

CLASS III.

Union in Pectoral Region, the Inner or Adjacent Pectoral Fins not being represented.[1]

Pl. II. figs. 7, 8 (external appearance); Pls. XV.-XVI. figs. 52-55 (horizontal sections); diagrams of various structures in Pl. XVII. fig. 63, XIX. fig. 75, XX. fig. 87.

Structures completely doubled. The brains, organs of sense, cranial skeletons, and anterior portions of the vertebral column are completely double and separate, as also are the two visceral arch systems, except for union on the part of the dorsal ends of the inner or adjacent last, and sometimes second last, branchial cartilages.

The general appearance is illustrated in Pl. II. fig. 7. It will be seen that the twin bodies do not meet in perfectly simple lateral union, but tend to come together first by their ventral aspect. This tendency, however, is not strongly marked, and is easily corrected at the transitional region, behind which the body has a normal bilateral structure.

Notochords, etc. The notochords and spinal cords are still widely separate opposite the pectoral region. They remain separate to near the 32nd body-segment, but ultimately fuse, so that the posterior part of the body and the tail contain a single notochord and a single spinal cord. The union of the spinal cords is well in advance of that of the notochords.

[1] See footnote on p. 11.

The behaviour of the neural and haemal arches and of the median muscular mass corresponds to the description on pp. 13, 15. These structures, however, may be studied to greater advantage in the type at present under consideration, as the whole transitional region is open for observation. The ventral ends of the two coraco-scapular bars fail by a wide interval to meet each other below the pericardium.

Alimentary Canal. The gullets and stomachs are separate, but union is found to take place (in the specimens sectioned) at the very commencement of the small intestine. The liver forms a single mass transversely drawn out and showing, on either side, the ramifications of separate bile ducts. The two ducts unite just prior to opening by a single aperture into the small intestine.

Heart and Vessels. Much interest centres round the heart and blood-vessels. A reconstruction drawing of the heart and origins of the vessels of a typical specimen of this group is given in Pl. XIX. fig. 75. The whole of this double heart lies inside a large composite pericardial cavity, which is prolonged a little forwards on either side round the origin of the ventral aorta. The ventricles are separate, the auricles communicate with one another, and there is a single large sinus venosus opening by a wide ostium into the auricles at their junction. The sinus venosus receives blood (*a*) on either side from the duct of Cuvier formed by union of the outer cardinal and internal jugular veins of the twin embryos (*i.e.* from the right duct of Cuvier of the right embryo and from the left duct of Cuvier of the left embryo); (*b*) from two separate middle jugular veins; and (*c*) from a large trunk formed by union of the inner or adjacent internal jugular veins of the twin heads. This last trunk obviously corresponds to fused adjacent ducts of Cuvier which receive anterior cardinal veins only and have no corresponding posterior cardinals. The hepatic veins also enter the sinus venosus, from below, but are not shown in detail here, their relations having been obscured owing to injury to the liver during removal of the yolk sac.

Kidneys. The head-kidney of a specimen belonging to this class is illustrated in Pl. XX. fig. 87. It resembles the type described under Class II. (p. 18).

CLASS IV.

Union in Pectoral Region, the Inner or Adjacent Pectoral Fins being present but united and reduced in size.[1]

Parts completely doubled. Doubling extends so far back that the two heads and the gill arch regions are entirely separate.

Ventral Convergence. The tendency to ventral convergence of the sagittal planes of the twin bodies now manifests itself somewhat strongly, and leads to slightly earlier union on the part of certain ventral than of dorsal structures. Thus the dorsal fin, while sometimes single along its whole length, is in other instances doubled anteriorly, although the ventral structures are all single at a corresponding level. The pelvic fins always form a single pair.

Notochords. The degree of ventral convergence is not so great that it cannot become rectified in the posterior body region, which, accordingly, exhibits a normal bilateral structure. This condition is finally established at, or near, the 36th body segment. Neural and haemal arch cartilages are disposed as already described for Class I. (p. 13).

Spinal Cords. Anteriorly the spinal cords are further apart than the notochords, but at the transitional region they rapidly approach each other and finally succeed in uniting, two or three segments in front of the notochords. The united part is at first composite, and shows the characteristic features already described (p. 17).

Inner or Adjacent Pectoral Fins. In typical specimens belonging to this class, fusion of the pectoral limb-cartilages tends to be more complete towards the posterior, than towards the anterior, border of the fins. Thus, in the specimen from which Pl. XVIII. fig. 66 is taken, near the anterior border there is only a small bridge of cartilage between the fins; further back the connecting bridge is broader but shorter; while at the posterior border the limb cartilages are united along

[1] See footnote on p. 11.

their whole length. As regards the inner or adjacent coraco-scapular bars, they are quite separate, except at their ventral ends, which join together and project downwards into a septum between the two pericardial sacs. The ventral ends of the two outer coraco-scapular bars are very widely distant from one another.

Heart and Vessels. The same specimen may serve to illustrate the typical arrangement of the heart and vessels in this group. There are two pericardial cavities separated by a septum of connective tissue, which is thin posteriorly, but in front is thick and contains the fused ventral ends of the adjacent coraco-scapular bars just mentioned. Auricles and ventricles are completely separate, and the sinus venosi communicate only by a narrow neck. Each sinus venosus receives a pair of ducts of Cuvier, the inner or adjacent ducts being smaller than the outer. This difference depends mainly on the fact that the inner or adjacent posterior cardinals are small and short. They can be traced backwards inside the substance of the head-kidney, but are soon found to unite and to break up into venules in the lymphoid tissue (Pl. XIX. fig. 74).

Kidneys. The glomerulus of the head-kidney is shown in Pl. XX. fig. 86. It is greatly elongated in a transverse direction. The tubule from its middle compartment, representing fused adjacent Wolffian ducts, passes forwards so as to lie between the two adjacent cardinal veins which have just been referred to. It ends blindly and is so much sacculated as to suggest a certain degree of pressure in the fluid secreted by the glomerulus. A similar point will be noted later (page 21), where one of the urinary bladders in a double monstrosity has no urinary pore.

Alimentary Canals. The gullets, stomachs, and first portions of intestine are separate, union taking place a short distance beyond the duodenum. There are two bile ducts and livers, the latter, however, being confluent on their adjacent sides. The dorsal mesentery of the intestine remains double for a considerable distance after the intestinal canals have united. A mesial triangular pocket or body-cavity thus lies dorsal to the first single portion of intestine.

CLASS V.

Union by the Body or Tail, the United Portion ending, as normally, in a Single Symmetrical Tail.

Pl. II. fig. 9 (external appearance, one of the components reduced); XVII. fig. 63 (notochords, etc.); XIX. fig. 77 (Wolffian ducts, etc.).

Ventral Convergence. At the beginning of the description of Class IV., ventral convergence of the sagittal planes of the twin bodies was referred to as a factor interfering with simple lateral union at the region of transition. In the class at present under consideration this factor is better marked and operates in a higher degree. Instead of simple lateral union we have a condition which is typically found in Schmitt's[1] group D (union half lateral and half ventral) (p. 3), but which is exhibited also by those examples of his groups C (union chiefly ventral but partly lateral) and E (union chiefly lateral but partly ventral) that approach nearest to the border line between their own groups and group D.

Roughly speaking, the degree of interference with bilateral symmetry is to be measured by the distance backwards at which union takes place, the difficulties in the way of simple adjustment being greatest where union is longest deferred. This will be seen to be only natural if one remembers that, to begin with, the twin embryonic axes appear tangentially on the surface of the yolk sphere and are situated far apart from one another on the margin of the same blastoderm (pp. 6-7). My classification is based simply on the final result, *i.e.* on whether the ventral convergence ultimately becomes rectified or not. In Class V. rectification does take place and is so complete that, ventrally, only one pair of pelvic fins occurs and the anal fin is single along its whole length, while dorsally the adipose fin is single and the spinal cords complete their union almost as early as the notochords. The dorsal fin, however, is partly or completely double. The level at which the notochord becomes

[1] Schmitt's paper (*216*) describes carefully and at length the structure of examples of Classes V. and VI., and may with advantage be referred to, for supplementary details.

normal varies somewhat, but may be put down at from the 38th to the 46th body segment. As regards the caudal veins and arteries, in one particular specimen the former united five segments in front of the vent, and the latter in the second pre-anal segment.

Intestinal Canals. As a rule, the twin intestinal canals become united a considerable distance (9-11 body segments) in front of the vent, the united portion being provided with two dorsal mesenteries which come from below the two notochords. More rarely, union of the intestinal canals takes place a few segments (6-4) in front of the vent, and I have not come across a single example of Class V. in which the intestinal canals are separate along their whole length.

Kidneys. The two head-kidneys are quite apart from one another, each being normal and giving rise to a pair of Wolffian ducts. As a rule, the inner or adjacent ducts end blindly in the mesonephric region, often being distended as if by the pressure of excreted fluid (Pl. XIX. fig. 77). In one example the inner or adjacent ducts open into a much swollen bladder which, like the anterior one in Pl. XIX. fig. 79, is destitute of an external opening. The outer Wolffian ducts on either side pass backwards as the right and left ducts of the single portion of the body, and open into a urinary bladder which communicates with the exterior by the usual single opening behind the vent.

Number. The number of double monsters belonging to this Class is relatively small. My material only provided five examples, in contrast with over twenty which fell to be included in Class VI.

CLASS VI.

Union by Posterior Part of Body, the united portion ending in a Composite Triangular or Quadrangular Tail, in which various structures are still doubled.

Pl. II. figs. 10-12 (external appearance); VI.-VII. figs. 27-31 (transverse sections); XIX. figs. 78-81 (Wolffian ducts, etc.).

The class is characterised either by (*a*) very marked ventral convergence of the two sagittal planes, or by (*b*) pure ventral union of the twins. Both of these conditions make it impossible for inner or adjacent structures to disappear gradually at the region of transition, and to leave just the complement of outer structures needed to make up a single bilateral region, as occurs in the earlier Classes, in the manner which has already been abundantly illustrated.

CLASS VI. (*a*).

This division includes all the well-marked and typical members of Schmitt's group C (union chiefly ventral but partly lateral). The posterior part of the body and the tail are characteristically triangular, there being two dorsal edge membranes and a single composite ventral edge membrane (Pl. VI. figs. 27-29; VII. fig. 31). The latter is produced by the coming together of the outer halves of twin ventral structures from which the inner halves have gradually disappeared.

In the earlier and middle members of this division there is only a single pair of pelvic fins, which is situated on the ventral aspect of the composite body and is itself composite in the sense that its units represent the outer pelvic fins of the twin embryos. The vent opens behind these. In the later members of the division the corresponding inner pelvic fins may be also represented, forming a pair on the upper aspect of the monstrosity. They are reduced in size, and either set close together or actually united with one another.

Notochords. The notochords either unite a varying number of body segments (12 to 1) in front of the rapidly thinning terminal "heterocercal" portion, or they unite in the heterocercal portion itself. The difference depends on how closely the ventral convergence of the sagittal plane approaches to direct ventral union, delay being naturally greatest as the latter condition is neared. However, even in extreme cases, the notochords always unite an appreciable distance in front of their actual termination. There thus remains a longer or shorter common pointed portion the tip of which always tends to curve in the mean dorsal direction, that is away from the ventral edge of the triangular tail. The caudal veins unite near the level of the vent and the caudal arteries several segments further back.

Spinal Cords. For the first three-fourths or so of the transitional region the spinal cords are always wider apart than the notochords. This condition persists in cases where the notochords unite in the heterocercal part, so that, here, union of the spinal cords is later than union of the notochords. However, when the notochords come together earlier, *i.e.* in the neighbourhood of the 12th last body-segment, the spinal cords may approach each other suddenly towards the end of the transitional region, in such a way that they finally unite with one another as early as the notochords. In no instance of Class VI. (*a*) did the spinal cords or the notochords fail to unite ultimately.

Intestine. The intestinal canals may unite anywhere within the last six or seven pre-anal segments, but do so usually quite close to the vent. As in previous classes the united portion has a double dorsal mesentery. The vent itself is always single.

Kidneys, etc. The Wolffian ducts, the bladders, and the urinary pores exhibit a number of variations, and will most conveniently be described along with the corresponding organs, under Class VI. (*b*).

CLASS VI. (*b*).

In the ventral union characteristic of this division, the tail shows four angles or keels which are continued more or less regularly right to the end of the caudal fin. Of these keels, two (one opposite to the other) are simply the dorsal edge membranes belonging to the mid-dorsal lines of the component tails. The other two, also opposite to one another, are ventral edge membranes and of composite derivation, half of each belonging to each twin. The manner in which these composite edge membranes are formed may best be understood by supposing that the blastema destined for the ventral portion of each embryo has been split into widely separated halves, and that in the process of *primary* fusion two new wholes (of composite nature) have resulted from the union of halves belonging to different embryos. A quadrangular tail with two (normal) dorsal and two (composite) ventral edge membranes is shown in Pl. VII. fig. 30. A comparable result is seen in the tail of the triple monstrosity, sections of which are shown in Pl. VII. figs. 32-4.

There are two pairs of pelvic fins, *i.e.* a pair in front of each of the composite ventral edge membranes on opposite sides of the quadrangular body. Obviously, each pair of fins is made up of components which belong to different embryos. Usually one of the pairs is smaller and more closely set than the other, and in such cases the vent, or pair of vents, opens behind the larger pair. Occasionally what should be the smaller pair is deficient altogether. In the remarkable specimen from which Pl. XIX. fig. 81 is taken, the two pairs of pelvic fins are exactly alike. This provides an instance of perfectly symmetrical ventral union.

Notochords. As regards the notochords, the rule is that they should unite for the whole, or for part only, of their thinner terminal "heterocercal" portions, each of which tends naturally to bend dorsalwards in its proper sagittal plane. When the portions in question unite at their commencement, the two opposing tendencies to dorsal flexure neutralise one another so that the united portion may project straight backwards. When union takes place near the extremity of the "heterocercal" portions, a certain amount of divarication may always be noted before these bend round to meet one another. This divarication is due to the fact that the tendency towards dorsal flexure has had scope for some degree of independent manifestation in each of the notochords. My own material has not furnished me with any examples in which the notochords never united, but instances of the kind are stated to occur by Schmitt (*216*).

Spinal Cord. The spinal cords either unite the shortest possible distance in front of their extreme posterior ends, or they never unite at all, and their union is typically later than that of the notochords.

Alimentary Canals. Three variations may be found: (1) Union occurring within the last three or four pre-anal segments; (2) two separate vents opening side by side in front of one of the composite ventral edge membranes; (3) two separate vents opening on opposite sides of the body, one in front of each of the composite ventral edge membranes. In the first instance the dorsal mesentery is double along the whole length of the united portion; in the second instance the two anal openings lie in a common field, and the last parts of the two recta are surrounded by a common

connective tissue sheath. The third variation is the most interesting, and it is illustrated in Pl. XIX. fig. 81. Here the union of the twin bodies has been so directly a ventral one, that the separation of ventral blastema (referred to above in connection with the formation of the composite ventral fins) has affected also the walls of the last portion of the rectum, as well as the anal pits. The two vents are accordingly to be looked upon as being composite structures. As will be seen from the figure just quoted, the Wolffian ducts, bladders, and urinary pores have undergone a corresponding rearrangement.

Wolffian Ducts, etc. Very great variation is found in the arrangement of the ureters, bladders, and urinary pores in Classes VI. (*a*) and VI. (*b*). All my specimens have two bladders, which sometimes communicate with one another and sometimes are quite separate. In practically all cases, the right ureter of one twin and the left ureter of the other open into one of the bladders, while the two remaining ureters go to the second bladder. Thus, each bladder receives a right and a left ureter derived from different embryos, and, except in cases of symmetrical ventral union, the ureters which go to the one bladder may be recognised as the inner or adjacent pair, while those which go to the other may be recognised as the outer pair. In such cases, the first bladder lies anterior and ventral to the second, with which also it frequently communicates, especially when destitute itself of an external opening.

Attention may be drawn to Figs. 78-81 on Pl. XIX., which are reconstruction diagrams illustrating the principal variations referred to above. Fig. 78 is drawn from a specimen in which the bladder in connection with the inner or adjacent pair of Wolffian ducts has no urinary pore, but opens into the bladder connected with the outer pair of Wolffian ducts. Fig. 79 illustrates a case in which the first bladder has no opening and is enormously expanded, as are also the lower ends of its ureters. Fig. 80 is from a specimen in which the bladders are separate and have urinary pores which open in the mid-ventral line, one behind the other. It will be seen that, in this case, the two bladders lie in the same plane and have corresponding right and left sides. But the right side of BL′ is in connection with a left Wolffian duct, while the left side is in connection with a right Wolffian duct. Such a transposition is exceedingly rare in double monstrosities. Two further variations are noted by Schmitt (*216*), namely an instance in which there was a single large bladder bifurcating into two horns, one for each embryo, and an instance in which all four Wolffian ducts opened by separate pores after each had widened out into a small bladder-like dilatation. Fig. 81 of Pl. XIX. is taken from the case of symmetrical ventral union already selected for special reference, inasmuch as the alimentary canals are united posteriorly, but open by two vents on opposite sides of the body. Two urinary pores are also present, one behind each of the vents. In this case, accordingly, the vents and the urinary pores lie in a plane at right angles to the sagittal planes of the twin bodies. This arrangement has many parallels in teratology, *e.g.* in cases of ischiopagous double monstrosity in the higher animals. It preserves the natural correspondence between rights and lefts in the ducts and bladders, which, as has just been seen, is inverted in the case of which Fig. 80 provides an illustration.

Caudal Vessels. Traced posteriorly, the caudal veins usually unite behind the vent or vents, and then divide into two vessels which pass backwards in the new plane of symmetry mentioned above, and are equal or unequal according as the type of union is purely ventral or not. The caudal arteries are similarly disposed, their place of union being, however, a short distance behind that of the veins.

CLASS VII.

Anakatadidymi (*Doubling at Anterior and Posterior Ends*).

A typical example is illustrated in Pl. I. fig. 2. Fig. 3 of the same plate shows a second example, which presents the very interesting anomaly that one of the twin heads shows the condition of semi-cyclopia (p. 44).

The anakatadidymi have to be subdivided into the two following groups: (1) with union by the walls of the yolk-sac only; (2) with union by the walls of the yolk-sac and, in addition, for a short stretch behind that region, by contiguous ventral structures. Examples of the second group

are very rare. I have come across none, and must borrow the following details from a description by Schmitt (*216*, pp. 52-3). The pre-anal edge-membranes are not united, and accordingly a triangular gap is left immediately behind the yolk-sac. Union of the ventral edges of the bodies occurs at the level of the vent, and is continued backwards throughout the first portion of the anal fin. Apart from this, the two tails are quite separate, one of them overlapping the other. There are two vents, close together, both looking towards the same side. Four urinary pores are present, each of the Wolffian ducts having remained independent and developed a small bladder-like dilatation near its posterior end. All four urinary pores open near one another just behind one of the vents. In other respects this small second group exactly resembles the first or main one, in which there is union by the yolk-sac only, and, accordingly, apart from the details just given, the following general description applies to both.

The twins tend to rest on their sides (Pl. I. figs. 2-3), the right side of one and the left side of the other being for the time uppermost. Sometimes the twin bodies are so exactly opposite to one another on the yolk that their sagittal planes coincide, and it then becomes a matter of indifference which sides are uppermost. In such cases, on external examination, an equal area of yolk will be visible in either position, and if the circulation be watched, each embryo will occasionally be found to possess right and left anterior yolk-veins of approximately equal size. The yolk store disappears on both sides at an equal rate, and leaves the twins united exactly opposite to one another by their ventral walls.

Sometimes, however, the embryos do not lie on exactly opposite meridians, so that their sagittal planes do not quite coincide. Accordingly, a rather larger area of free yolk will be visible between the twins on one side as compared with the other. They still come to rest on their sides, but now those sides tend to be underneath between which the area of free yolk is the larger. Towards the end of its absorption the yolk is visible on this aspect rather longer than on the opposite one.

In healthy twins the movements of breathing go on at equal rates, and it would appear that these movements are usually synchronous, but this rule is by no means without exceptions. The frequency of cardiac pulsation also tends to correspond in the twin hearts, but, as a matter of fact, the individual beats are independent, that is neither necessarily synchronous nor alternating with one another. This same point was observed by de Quatrefages in the double-headed shark which he described and figured (*198* Pl. VIII. figs. 1, 2).

Coste's view (*43*) that in double monster fish the hearts aid each other in maintaining an active circulation by having an alternate rhythm does not apply to healthy specimens, though possibly it holds good in cases where one embryo is degenerating and about to become parasitic on the other.

Over the yolk-sac, free anastomosis occurs on the part of the finer vessels belonging to the two embryos. Usually also, the anterior yolk-veins are connected by one or more larger anastomotic branches, but on the whole, each embryo keeps the major part of its own blood to itself. The arrangement of the yolk-veins presents many variations. Each embryo tends, however, to have a right and left yolk-vein, but these are seldom of equal size, and one or other of them may be absent. A furrow on the anterior aspect of the yolk-sac commonly marks the boundary between the two circulations.

It was this furrow which Quatrefages and others interpreted as indicating the fusion of two separate yolks. The furrow is not visible at all in very young double monsters, and is only well marked during the middle stages of yolk absorption. After absorption of the yolk is completed, the body cavity shows a large mesial common chamber, which is prolonged backwards and forwards within each embryo, thus forming four horns. The intestinal canals are quite separate, and probably also, as a rule, the livers. Union of the ventral body-walls exists from just behind the breast fins to a short distance in front of the pelvic fins. The right and left abdominal recti in each embryo become separated from one another as they approach the region of union, and then each arches backwards, keeping to its own side of the junction line. Reaching the hinder

end of the united region, the individual right and left reeti next rejoin one another within their proper embryos, in which they are continued backwards to their posterior termination (Schmitt *216*).

The following points relating to anakatadidymi receive mention elsewhere:

Frequency of occurrence, p. 7; relation to homologous twins in higher animals, p. 7; survival after exhaustion of yolk, p. 2; orientation of the developing embryonic axes, p. 7.

CLASS VIII.

Hemididymi (*Mesodidymi and Katadidymi*).

Under these terms are grouped certain forms which are due to similar developmental aberrations, and present a characteristically imperfect degree of duplicity. In mesodidymus there is apparent doubling of the middle region of the body, the anterior and posterior ends being single, while katadidymus is marked by apparent posterior duplicity.

As far back as 1863, Lereboullet (*143*), dealing with living material at very early stages, described various examples taken from the pike. Careful descriptions were afterwards given by Oellacher (*176*) of more advanced stages in *Salmo salvelinus*, examined both superficially and by the method of serial sections. This author proposed the term *mesodidymus* as being supplementary to ana- and katadidymus already introduced by Förster. Rauber (*202* **5**) next added a description of very early specimens in *Salmo fario*. He had previously suggested that Oellacher's specimens should be called *hemididymi* to indicate the imperfect character of the doubling which they exhibited (*200* **71**).

Almost from the first, the problem of the origin of hemididymus was closely connected with the theory of concrescence. Lereboullet enunciated this theory, practically though not formally, in the course of his observations on the pike. Oellacher did not consider it needful to adopt the theory in question, which had meantime been definitely formulated by His. Rauber was a supporter of concrescence, which seemed to him to be alike confirmed by, and explanatory of, the hemididymous condition. Later, the experimental work of various observers, notably Kopsch (*132-133*), Morgan (*162*), and Sumner (*242*), settled the major question of concrescence in the negative for fishes (see below, p. 27), and at the same time threw much light on the origin of the abnormalities at present under consideration. These have also received illustration from the study of similar defects in other animals, particularly in the Amphibia.

Structure. We may begin with a summary for mesodidymus as described by Oellacher (*176*) in *Salmo salvelinus*. There is more or less complete doubling throughout a longer or shorter portion of the middle region of the body, while the anterior or posterior ends both externally and internally are perfectly single. The complete doubling involves the mesial organs alone, namely the nervous system, the notochord, the gut, and also in certain cases the liver. On the other hand, all the lateral paired organs, namely muscle plates, Wolffian ducts, auditory organs, and peritoneal cavities, are present only in the total number characteristic of a single embryo. They lie on the outer side of the twin embryonic axes, and are deficient (except for occasional rudiments of the muscle plates) on the inner or adjacent sides. The duplicity of the central nervous system and of the notochord always extends further back and further forward than that of the gut. The length of the hiatus or space between the two components varies greatly. It may only affect the middle of the body (and that not very deeply), or it may affect the whole body from the mid-brain region right back to deep in the tail. In early stages while the yolk-sac is large, the breadth of the space between the components varies proportionately to its length, but in later stages when the yolk is absorbed the twin axes come to lie close to one another, and the space in question is reduced to a very narrow slit, the bodies at the same time becoming greatly contorted.

In the floor of the hiatus, the yolk appears, not with a free surface, but covered by ectoderm, beneath which a thin sheet of mesenchyme containing blood-vessels seems also to occur. At the posterior end of the hiatus there is nearly always to be found a peculiar tubercle, made up of large epidermal cells, and situated just in front of the place of union of the two spinal cords.

Oellacher also observed and described several specimens showing posterior duplicity (katadidymi). In these specimens the division, instead of being confined to the middle of the body as in mesodidymus, is carried back through the tail region. The posterior part of the body and the tail are accordingly doubled, although the doubling still remains of the same imperfect kind which has been described above as characteristic of mesodidymus. The most complete example of katadidymus recorded by Oellacher is one in which the duplicity begins as far forward as the region of the optic lobes. Variations of the typical condition are noted, for example the two components may be unequally developed, one of them being short, defective in parts as regards the notochord and other structures, or even completely interrupted. Or again, small *inner* muscle plates may be present at various points.

In the pike, Lereboullet (*143* **20** p. 218 *et seq.*) described thirteen instances of mesodidymus, and two of katadidymus. As regards mesodidymus, his first example and the example which he illustrates in Pl. III. figs. 26, 28, are perhaps the most important. The former was observed on the sixth day after fertilisation, and lived till about the fifteenth day, but never hatched out. The fore part of the head was single, but mesial separation began as far forward as the optic lobes, and continued back to the tail, which became normal. The two components were somewhat unequally developed, but each had a notochord as well as a spinal cord and an outer set of muscle plates. Remarkable features in this specimen were the presence in each component of a heart and of a small inner otocyst besides the large outer one. The hearts commenced to beat regularly. Inner otocysts did not occur in Oellacher's specimens of the trout. He and Rauber suggest that Lereboullet's observation is likely to have been a faulty one. It seems to me, however, that the formation of small inner otocysts is just as likely to occur as that of occasional small inner muscle plates.

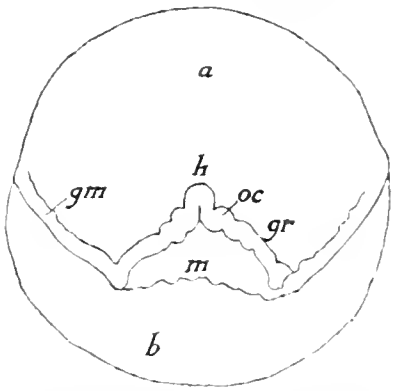


FIG. 4.—After Rauber (*202* 5, Pl. XLI. fig. 19). An extreme example of the hemididymous condition (*dehiscence*, Rauber), in an egg of the trout sixteen days after fertilisation. *h*, the bending round anteriorly of the germinal thickening *gr*; *oc*, region of the primitive optic outgrowths; *m*, membrana intermedia; *a*, blastodermic surface; *b*, surface of yolk uncovered by blastoderm; *gm*, margin of blastoderm.

The example illustrated by Lereboullet in Pl. III. figs. 26, 28, is interesting since it shows the presence of a thin membrane lying between the divergent components and covering the yolk. The latter, however, still appears through a small round gap in the membrane at the place where overgrowth is just about to be completed. We may compare this with the covering membrane described by Oellacher, and we must assume that here the advancing blastodermic margin has consisted of epiderm only.

Rauber (*202* 5 pp. 694-699) described six early examples in *Salmo fario*—all of them evidently katadidymi. One is at a stage sixteen days after fertilisation. Normally at this stage the various regions in brain and body are beginning to be definite, and the outgrowth for the tail is raised up from the surface. The specimen in question shows dehiscence of the two halves of the embryo from the origin of the optic vesicles backwards (see Text-fig. 4 on this page). Almost symmetrical markings occur on the two sides of the gap and indicate corresponding differentiating cerebral structures. Posteriorly, on either side, a small tubercle is seen which the author thinks must represent the separated halves of a tail bud. The hiatus between the two body-halves is bridged over by a thin layer of ectoderm—the *membrana intermedia*—resting on the *primary entoderm*, or yolk with nuclei but without separate cells. The definitive entodermic layer is, of course, awanting.

Of the other five cases described by Rauber, one also exhibits dehiscence affecting the whole length of the body, but in the rest, the dehiscence affects the middle and posterior parts only. One of these is of particular interest, since it shows a gap interrupting the continuity of the right component.

Kopsch (*132*) succeeded in producing two hemididymi in eggs of the trout by applying electrical

stimulation immediately behind the embryonic rudiment. In one example, the body-halves commenced to separate in front of the first muscle plates, while in the other the separation began at the anterior border of the auditory vesicles. An outer series of sixteen to eighteen muscle plates was present in each component in both cases. At certain places small *inner* muscle plates were found, while various portions of the notochords were absent or defective. The presence of inner muscle plates in the one component corresponded, on the whole, with their absence in the same region of the other component. There was similar mutual correspondence between normal and defective formation of the notochord in the two components.

Moser (*165*), who lays stress on these alternations, would seek to throw light on the structure of hemididymi in general by supposing that three kinds of fission on the part of the growing embryonic axis may take place, viz. (1) *ordinary equal*, producing similar components; (2) *ordinary unequal*, producing components one of which is larger than the other; and (3) *zig-zag*, producing components with certain alternating structures.

References to minor abnormalities observed by the author, and traceable to mesodidymus or katadidymus, will be found on pp. 52, 54 of the present work.

Causation. Mesodidymus and katadidymus in fishes may be produced experimentally through the same kinds of agencies as cause defective conditions in general. Thus Knoch (*127*) found duplicity of the posterior kind to occur much more frequently in eggs hatched out in water which was stirred up by an active current than in still water. Jablonowski (*106*) was able to produce splitting of the embryonic rudiment by the action of common salt solutions. A similar result occasionally appeared in Stockard's (*236* p. 105) experiments with lithium chloride, and Kopsch (*132*) induced the formation of two hemididymi by electrical stimulation.

A satisfactory account of the mode of origin of hemididymus can, however, hardly be given at present. Probably the condition may result from different factors. Before discussing these, it will be necessary to refer again briefly to what is known regarding the earliest stages in the formation of a normal embryo.

Kopsch's experiments seemed to show that the embryonic blastema for the head and body is spread out, to begin with, over a small segment of the blastodermic margin, the head blastema occupying a middle position and being flanked on either side by the body blastema, which is thus divided into two separate masses. Next, the two masses of body blastema come together behind that of the head, and, having united, grow backwards. The region formed by their actual union is called by Kopsch the *primarily formed portion* of the body, and we see that it has resulted from a very limited sort of concrescence. It produces the rest of the body by backward growth, and, as was stated on p. 6, during this growth material is drawn from the adjacent thickened margin of the blastoderm for the formation of the lateral and ventral body-walls, and in particular for the muscle plates.

On the other hand, Morgan (*161*) and Sumner (*242*) hold that the blastema for the whole embryo is disposed from the first in a spatially single centre, and that this centre produces the definite body and tail by backward growth, accompanied by utilisation of material from the thickened adjacent margin of the blastoderm in the manner already noted. These authors, accordingly, deny even the limited degree of concrescence which Kopsch would admit.

If we adopt the view of Morgan and Sumner, we may look on hemididymus as capable of being produced either (A) by factors which tend to *draw* apart into two diverging horns the backwardly growing mass of blastema which should give rise to a normal body or tail; or (B) by factors which hinder the direct backward growth of the blastema in question, causing it to *split*, so to speak, into two streams which flow round the obstacle; or (C), by any of the causes, innate or external, which tend towards excessive growth and fission on the part of a growing system.

If we adopt Kopsch's view as to the mode of formation of the embryo we shall have to say in addition that the causes detailed under (A) and (B) may operate at the very start by preventing concrescence on the part of the masses of blastema from which the *primarily formed portion* of the body arises.

(A) Seeing that material is drawn in considerable amount from the adjacent margin of the blastoderm on either side to aid in the formation of the lateral parts of the body, any cause which fixes this material or diminishes its mobility will induce a corresponding outward pull or drag on to the two sides of the embryonic rudiment. This may well be strong enough to make the growing end of the rudiment divide into two horns, each of which would then naturally proceed to grow backwards and would attempt to become complete and bilateral in itself, according to a potentiality which seems to be inherent in all embryonic apical systems. Completeness on the inner or adjacent sides would not be attained, however, there being no material at hand to aid in the formation of the muscle plates on these sides. Under normal conditions it is the gradual extension of the blastoderm enclosing the yolk which continually brings the required marginal material into serviceable position, and accordingly any condition which prevents the spreading of the blastoderm or increases the area to be covered may cause the pull or drag referred to above. Hemididymus may therefore be expected to appear (1) in ova the vitality of which has been lowered from any cause, *e.g.* hatching under unfavourable conditions, as in agitated water, in water deficient in oxygen, or having foreign substances in solution, and (2) in ova which have become partially swollen through differences of osmotic pressure or other cause. It is a common occurrence in ova with lowered vitality that definite organs are the first to suffer, whilst the undifferentiated superficial blastoderm, and later even the mesenchyme, may continue to spread. Here we have a possible explanation of the fact brought out by Lereboullet, Oellacher, and Rauber, that a thin epidermal layer bridges the space between the diverging halves of the body, and also of the additional fact noted by Rauber that the underlying yolk in this region contains nuclei without cell boundaries, *e.g.* that the primary entoderm may be present although the definitive entoderm is never formed.

The thickened ectodermal tubercle noted by Oellacher at the posterior angle of the cleft between the two body-halves in mesodidymus is difficult of explanation, but may perhaps be due to the crowding together of surface tissues which will naturally take place in the angle of re-union, and which will be augmented afterwards through the supervention of secondary fusion. That the last named process occurs in an appreciable degree is evidenced by the fact that the doubling of the notochords extends very considerably further back than doubling of the spinal cords, or of the alimentary canals.

(B) The factors grouped under (B) have to do with postero-mesial obstruction or defect, and this may be caused by mechanical injury to the yolk or to the tip of the growing tail bud. The hemididymi produced by Kopsch (*132*) through electrical stimulation were no doubt of this kind. Each of the divisions thus produced will attempt to complete itself as described under (A), but here again the absence of a supply of lateral material on the inner or adjacent sides prevents the realisation of the perfect bilateral condition.

Alike in (A) and (B) the two axes will now naturally follow in their growth the thickened margin of the blastoderm. If the extension of the latter has been greatly interfered with, the axes may never again be brought together, and thus the katadidymous condition may result. Or if vitality has been only slightly lowered, the axes may become approximated posteriorly, through delayed completion of the natural process whereby the yolk is covered. The tail buds now becoming united may give rise to a single posterior portion, and thus the mesodidymous type described by Lereboullet and Oellacher will result.

(C) Mention of the causes under this heading is made on chiefly theoretical grounds, since observations on their nature and action are awanting. But there is every reason for believing that the growing embryonic axis of a fish possesses that potentiality of fission which manifests itself from time to time in the growing axes of other vertebrates, as in apical growth-systems generally.

Rauber's "posterior radiation" theory attempts to express and formulate the potentiality in question, which was admirably enunciated by Cleland (*39*), as a principle even wider in its nature and application.

Prevalent Types of Monstrosity in Fishes and in other Vertebrates. The chief difference between fishes on the one hand and birds and mammals on the other, as regards the types of monstrosity

which they exhibit, is that in fishes posterior duplicity is rare, and when it does occur, is always of the imperfect hemididymous kind. By contrast, the other two groups both provide excellent examples of posterior doubling. In this connection, it should be added that no example of posterior triplicity is known among fishes, while undoubted instances of this condition have been recorded among mammals (see p. 39).

We have seen that the imperfect doubling characteristic of katadidymus in fishes arises in all probability from the circumstance that inasmuch as the posterior end of the embryo remains continuous with the edge of the blastoderm, the inner sides of a posteriorly dividing embryonic rudiment abut on the yolk, and, accordingly, are unable to obtain the peripheral cell material normally employed in building up the lateral and ventral body walls. For want of this, the two diverging limbs of the divided axis are unable to complete themselves by becoming bilaterally symmetrical in the full degree.

In birds, on the other hand, the groove of the sickle early becomes obliterated, the blastoderm spreading rapidly behind it. The posterior end of the primitive streak (and afterwards of the growing embryonic axis) is thus removed from the margin of the blastoderm, and lies entirely within the area of the latter. Should the posterior end of the primitive streak (or of the embryonic axis) for any reason undergo fission or dichotomy, the new growth-systems thus produced will find their inner or adjacent, as well as their outer, sides abutting equally on the various blastodermic layers. Nothing will then hinder the systems in question from completing themselves so as to become bilaterally symmetrical, in virtue of that power and tendency towards the realisation of *the whole*, which, as we saw reason above to believe, may be manifested at very early stages by all embryonic growth-systems should opportunity and necessity arise.

On the whole, the reptiles will tend to resemble the fishes as regards the types of monstrosity which they exhibit, since in them the primitive streak and the posterior end of the embryo maintain a modified continuity, for a considerable time at least, with the margin of the blastoderm. It is true that, as far as I am aware, no examples of the hemididymous condition have been recorded among reptiles, but neither (with one very doubtful exception [1]) are there any instances of true posterior duplicity. On the other hand, anterior duplicity is far from being rare, considering the relatively small numbers of reptilian ova and embryos that come under observation.

CLASS IX.

Longitudinal or Parallel Union.

My own material has not provided me with any examples of this class, and indeed the sole instance on record in the Salmonidae appears to be Barbieri's (*6*), which has reference to an egg of *Salmo irideus* fixed seven days after fertilisation and showing a double embryo 3 mm. in length.

There is a marked tendency for the organs of the ventral part of this embryo to show duplicity in a greater degree than the dorsal ones.

For example, the brain cavity in cross section looks like a three-rayed star. One of the rays is directed dorsally, while the other two point downwards and to the sides, and represent the ventrally-doubled central cavity. The spinal cord is triangular in section, and has a notochord below each basal corner, while ventrally and mesially a series of united inner mesoblastic somites is to be found. There are two pairs of optic vesicles, the inner ones being more or less fused together. One of the twin sides is rather smaller and less well developed than the other, the mesoblastic somites in particular being deficient in size. Two vesicles of Kupffer can be made out, the one belonging to the smaller twin being situated a little in front of the other. In the figures there is no sign of duplicity on the part of the gut.

It will be remembered (see p. 10) that one of the types into which Lereboullet classified

[1] A young blastoderm of *Lacerta ocellata* showing on a single embryonal shield two primitive streaks converging gently in front (Tur, quoted from Schwalbe *222*, II. p. 30).

his series of anomalous pike embryos is distinguished by the presence of a *single broad* embryonic rudiment showing more or less complete duplicity of the axial structures especially in front. No doubt this type approaches the anadidymous condition, but following Lereboullet's description one must infer that it will also include examples of parallel union.

Dohrn's (*57*) *Torpedo* embryo, of which a short account is given on pp. 31-32, seems an almost perfect example of the class. Unfortunately details are not available regarding the condition of the anterior and posterior ends of this embryo.

Mode of Origin. There is little evidence to go upon, but if, as seems certain, the class is really separable from the anadidymi, and therefore justifiable on logical grounds, we must assume that there has been, to begin with, a single centre of gastrulation, and that in connection with this centre there have appeared two sets of axial structures (notochord and nerve cord) lying parallel with one another. Ultimately, posterior union of these axial structures, or entire reduction of one set of them, cannot fail to occur during the progress of growth, since no reserve of cell material is available for the formation of inner or adjacent parts (see p. 6 and p. 27). In the end therefore the condition will become an anadidymous one, but from the disposition of the twin components, the tendency to loss or concealment of duplicity through secondary fusion will have the chance of operating very fully, and Lereboullet's observations show that this actually takes place.

DOUBLE MONSTROSITY IN OTHER FISHES.

Blennius. Rathke (*199*). An anakatadidymous specimen: two separate embryos, one larger than the other, the smaller joined to its neighbour and to the yolk-sac by a short connecting band (quoted from v. Baer *5* 89).

Cyprinus Blicca. v. Baer (*5*). Two anadidymi: (1) two heads united in neck region and diverging at an angle of 60°; (2) union behind the middle of the body, divergence at 110°. Both specimens were observed $2\frac{1}{2}$ days after fertilisation.

Scomber. Sutton (*245*). Mention of double monstrosity in the mackerel.

Anarrichas. Buckland (*33a*). A more than doubtful instance, referred to on p. 2.

Leuciscus. Bataillon (*11*) describes fragmentation of ova temporarily exposed to differences of osmotic pressure. This was followed by an attempt at independent development on the part of the fragments. The results, which were experimentally obtained, are of somewhat doubtful nature.

Girardinus Caudimaculatus. An example of anakatadidymus is recorded by Emeljanov (*65*) in this species. The twins were united together ventrally behind the second pair of fins by means of cutaneous structures. They were not so large as normal newly hatched embryos, one of them in particular being smaller and less active than its neighbour, to the movements of which it proved a hindrance. They lived for about a week after hatching.

Petromyzon. Bataillon (*12*) describes a particular group of about a hundred artificially fertilised eggs of the lamprey. In 40 per cent. of these the first segmentation furrow—a vertical one—went deeper into the substance of the egg than the later ones, so that the whole mass was to some extent divided into two halves by a vertical constriction. These halves gave rise each to a blastula and gastrula, the blastoporic openings being on the under side. In later development most of the eggs died off, but four managed to survive, twin larvae hatching out from each.

Experimentally Bataillon (*11*) succeeded in obtaining imperfect imitations of the above, by exposing lamprey eggs at suitable stages to temporary changes of osmotic pressure.

Selachii. There are a fair number of records relating to double monstrosity in the cartilaginous fishes. All are examples either of anterior duplicity or of union by the ventral abdominal walls (yolk-sac union). The proportion of the latter to the former is much greater than in the trout, namely, 1 to 2·25 in contrast with 1 to 13 (see p. 7). This is what might be looked for, considering the relative sizes of the blastoderms and yolks in the eggs of cartilaginous and osseous fishes. The tendency to *primary fusion* will operate over a smaller proportion of the whole blastodermic

margin. Taking the figures as they stand, they would mean that in order to remain separate the two embryonic rudiments would have to be located, to begin with, at an angular distance of not less than 129·5° from one another on the margin of the blastoderm. The corresponding distance in the trout, as estimated in the same manner, amounts to not less than 165° (p. 7).

Classification of Double Monster Cartilaginous Fishes.

Probably if a full series were available for comparison, the same types of double monstrosity would be found to occur in the cartilaginous as in the osseous fishes. The mode of origin will be essentially the same in the one group as in the other, and the degree of duplicity will again depend on the distance which originally separated the two embryonic rudiments on the margin of the blastoderm. On these points, however, we must speak by inference, since direct observations are awanting.

Altogether I have only been able to collate thirteen recorded instances in the cartilaginous fishes. The chances are that this number should be reduced to twelve or possibly to eleven, owing to duplications, no longer traceable, in the records. As a rule few descriptive details are given, even regarding external characters, and in no case is the internal anatomy adequately outlined. None of the specimens is described as katadidymous, although that figured by Gadeau de Kerville (see below) somewhat resembles the later stages of this condition in the trout. No instance of triplicity seems yet to have been observed except under experimental conditions (see note on p. 5). The records which I have been able to obtain are given below. In regard to some of the specimens, the species and even the genus cannot now be ascertained, but all such specimens may be put down as being sharks or dogfish.

Union in the Head Region. An example is figured by St. Hilaire (*213*, Pl. XIV. 5) in the atlas attached to his great work. The two inner eyes are close together, but do not seem to be actually united. As far as one can judge, inner spiracle-openings are absent. Probably the twin brains are united with one another towards the anterior part of the medulla.

Union in the same region or a little further back is perhaps exemplified by the instance recorded by Risso (*205*), in which two mouth-openings were present, one above the other. St. Hilaire, however (III. 202), throws some doubt on the validity of this record.

Union in Pectoral Region. Gadeau de Kerville (*73*, Pl. XVIII. figs. 1, 2). A young *Acanthias vulgaris* with the umbilical vesicle still well marked externally. Inner pectoral fins are not present. The posterior part of the body is irregular and distorted in a manner resembling, superficially at least, the condition frequently seen in advanced katadidymous trout embryos.

Union just behind the Pectoral Region. Quatrefages (*198* pp. 11-12) gives a careful description of a young *Acanthias* showing anterior duplicity. The union occurs just behind the pectoral region. Inner pectoral fins are present, the one belonging to the right twin being markedly displaced downwards, while the other is correspondingly displaced in an upward direction.

Union near the middle of the Body. Aldrovandi (*2*). The shark referred to on p. 2.

Heusner (*94* 8 p. 34). "Dr. Barclay of Edinburgh had a new-born specimen, double to the umbilicus, while there is a similar specimen in the Hunterian Museum" (quoted from v. Baer *5* p. 88).

Lowne (*146* p. 11 No. 23). A foetal dog-fish exhibiting anterior dichotomy. The dichotomy extends to the umbilical region, and the ventral convergence of the sagittal planes is so well marked that the component embryos may almost be described as facing one another.

Union by the yolk-sac only, or, after absorption of the yolk, by the abdominal walls.

Heusner (*94* 8 p. 34). "Professor Brookes in London had a specimen double anteriorly and posteriorly, but united in the middle of the body" (quoted from v. Baer *5* p. 88).

Levison. A sternopagous double monster (quoted from Panum *180* p. 72).

Lowne (*146* p. 11 No. 22) catalogues two small sharks united by the abdominal walls. The remains of a single yolk-sac is seen between the pectoral fins. The specimen was obtained from a female shark taken by the donor (mate of a vessel) in the Indian Ocean. When brought on deck

and cut up, about thirty living young escaped from its abdomen. The specimen presented lived for about two days in a bucket of water.

Klaussner (*123* p. 12) makes mention of an instance in which there were two embryos on opposite sides of the egg of a cartilaginous fish. The record was given verbally to him by Dr. Rückert.

Longitudinal or Parallel Union. Dohrn (*57*) describes and figures an interesting malformation in an embryo of *Torpedo marmorata*, one mm. in length. The specimen, which had been cut into horizontal sections, shows two notochords lying parallel with one another, and a short distance apart.

The mesoblast on the outer side of each notochord is normal in arrangement and shows division into seven muscle somites. Between the notochords is a narrow unpaired strip of mesoderm with eight separate somites, forming a series which is out of line with the normal lateral ones. Details are given regarding the size, etc., of the somites, but the condition of the nervous system and of the alimentary canal is not described.

Parasitism. No definite instances seem to be on record, but the suggestion is not an unreasonable one that the accessory fins noted by Gervais (*80*) and Rennie (*203*) in the skate are remains of rudimentary twins (see p. 54).

CHAPTER II.

TRIPLE MONSTROSITY.

Description of a specimen, - - - - - - - - - - - - p. 33
Other instances in fishes, - - - - - - - - - - - - p. 35
Mode of development in fishes, - - - - - - - - - - - p. 36
Appendix on Triplicity in other vertebrates, and on Classification in Germinal Triplicity, - - - - - - - - - - - - - - p. 37

DESCRIPTION OF A SPECIMEN.

TRIPLE monster fishes are extremely rare. In the trout, I have only come across one example, as contrasted with over seventy double forms. In birds, on the other hand, Dareste's figures show one example of triplicity to nineteen of duplicity, the latter condition in turn occurring on an average in one out of every two hundred and fifty eggs incubated.[1]

My specimen came from a brood of young trout which had been hatched for about five weeks, and were still subsisting on the egg-yolk. The general appearance is shown in Pl. XXII. fig. 94. Figs. 95-99 in Pls. XXII.-XXIII. and Figs. 32-34 in Pl. VII. also have reference to this specimen, and illustrate the alimentary canals, the Wolffian ducts, and various transverse sections. It will be seen that only one of the component embryos is properly developed. In what follows, this component will be designated the principal embryo. The other two, which may be called "A" and "B," are much smaller, and are defective in various important respects. Posteriorly they become united first with one another and then with the principal embryo in the manner to be afterwards described.

Principal Embryo. This embryo is slightly smaller than ordinary examples of the same age, but is otherwise normal except in the posterior fourth of its length, where it becomes distorted through the addition of tail elements belonging to the defective embryos. It retains along its whole length its own spinal cord, notochord, neural and haemal arch cartilages, muscle masses, aorta, caudal vein, and alimentary canal.

[1] It will be seen that in birds the proportion of triple to double monsters is thirteen times greater than the proportion of double monsters to normal forms. This fact seems to indicate that blastoderms with two centres of embryo formation show a greater tendency to exhibit a third centre than can be accounted for by the theory of probability applied to the results of simple random distribution. We may suppose that in ova generally there is a certain liability to the incidence of duplicity or multiplicity. The result is to produce a certain proportion of cases in which there are at least two centres of embryo formation. Within this latter group of cases it may naturally be expected that the incidence will show intensification if the liability be fundamentally due to a predisposition depending on inherent germinal factors. Dareste's figures indicate that such an intensification is actually present, the final result being that the ratio between double and triple monstrosities is so far lessened as to be approximately equal to the square root of the ratio between normal and double forms.

In the trout we do not possess so complete a series of observations dealing with early stages, as is that of Dareste for birds. However, Rauber (*202* **6** 139-184), examining a large number of ova ten to sixteen days after fertilisation, obtained one triple rudiment as compared with eighteen which showed duplicity. If we take 1 in 300 (see p. 1) as something like the average ratio between double and normal forms, it will be seen again that this ratio is approximately equal to the square of that indicated by Rauber's observations as existing between double and triple monstrosity. All this is in consonance with the view that the formation of double or multiple embryos has behind it something of the nature of germinal predisposition.

The distortion affects chiefly the ventral aspect of the tail and the tail fin. The ventral edge membrane (including the anal fin) may be described as having been split widely apart into two halves. These unite with a moiety from the corresponding structures of the defective embryos, to form two composite ventral edge membranes. (Compare with ventral union in double monstrosity, pp. 22-23.) A transverse section near the commencement of the tail (Pl. VII. fig. 32) shows five angles, viz. three referable to the dorsal edge membranes of the three embryos, and two to the composite structures which have just been named. Nearer the tail (Pl. VII. figs. 33-34) the number becomes reduced to four through fusion of the dorsal membranes of the two defective embryos.

The alimentary canal and the Wolffian structures are referred to, after the description of "B."

Defective Embryo "A." The cerebral lobes, the pineal body, and the 3rd ventricle region are entirely absent. The optic lobes are small and distorted, while the cerebellum, the 4th ventricle and the medulla are present but reduced in size. The spinal cord consists of irregular nervous tissue without a central canal, and is not separated by a membranous capsule from the surrounding structures. It joins the spinal cord of the other defective embryo a short distance in front of the vent. The united part becomes rapidly smaller, and disappears without passing back into the tail.

There is no trace of olfactory organs or of eyes, but two small otocysts are found lying against one another below the medulla. The left otocyst has a main chamber without distinction into saccule and utricle. It gives rise to a single large semicircular canal with an ampulla and crista acoustica, besides two other small pockets destitute of sensory cells. The right otocyst shows traces of division into saccule and utricle. The saccule has a sensory patch, while the utricle has one well-developed semicircular canal besides a small blind evagination.

A single small auditory nerve is seen passing down from the medulla between the adjacent surfaces of the pair of otocysts.

The notochord is absent except between the otocysts and for a short stretch below the medulla.

There are three or four irregular gill arches separated by slits and carrying gill tufts. Pectoral fins are present, but reduced in size. There is a small single pelvic fin on the right side.

The embryo is acardiac, and its tissues are supplied with blood from the yolk-sac vessels of the principal embryo.

Defective Embryo "B." The structures found in "B" are practically the same as in "A." The spinal cord, however, is even more irregular, and the left notochord is entirely absent. A single pelvic fin is seen on the left side of "B," and is in all probability a composite structure formed in conjunction with the principal embryo, in the manner already described for the ventral edge membranes.

The dorsal edge membranes of "A" and "B" are separate in front, but unite posteriorly, where they form one of the angles of the quadrangular tail fin.

Alimentary Canal and Urinary Organs. The monster has two vents, which lie close together just behind the pelvic fins of the principal embryo and of embryo "A." One of these leads into the intestinal canal of the principal embryo, which is entirely separate from that of the others. The second vent is the orifice of a portion of intestine common to "A" and "B." This common portion bifurcates anteriorly near the middle of the small intestine, giving rise to separate stomachs, gullets, air-sacs and livers, for the two embryos "A" and "B."

There is a single urinary pore behind the vent. This pore leads into a bladder which is common to all the embryos. The right Wolffian duct of the principal embryo has a separate opening into the bladder; the left Wolffian duct of the principal embryo and the right duct of embryo "A" unite before opening into the bladder, as also do the left duct of "A" and the right duct of "B." The left duct of "B" ends blindly.

The alimentary and the urinary systems are illustrated in Pl. XXII. figs. 95 and 96.

OTHER INSTANCES OF TRIPLICITY IN FISHES.

1. *Esox lucius.* An egg, observed four and a half days after fertilisation, showed two embryos uniting posteriorly behind the pectoral region, and diverging widely in front. The left component was normal, but the right one had two heads, the outer of which was somewhat defective. In later development the latter showed only a single eye, viz. its outer one. The specimen lived ten or eleven days and developed two hearts, one belonging to the left embryo and the other to the (doubled) right component. The two hearts were independent as regards pulsation (Lereboullet, *143* **1863** p. 217, Pl. III. figs. 24-25).

2. *Salmo fario.* This is a blastoderm showing three embryonic rudiments. Rather more than half of the yolk still remains uncovered. Two of the rudiments are extremely close to one another, and, indeed, are in process of uniting posteriorly. The third is at an angular distance of approximately 60° to the left along the edge of the blastoderm. This is the youngest triple Salmonid of which we have any record. Fuller development would no doubt have produced a form closely resembling the preceding (Rauber, *202* **6** p. 145, Pl. VIII. fig. 15). Text-fig. 5 on p. 56 of this work illustrates the specimen just described.

3. *Salmo salvelinus.* Also a very early example. Only 18 to 20 mesoblastic somites are present, and the yolk is not yet completely covered. The embryonic axis, which is single posteriorly, bifurcates in front, and the right branch again divides (Klaussner, *123* p. 31, Taf. VI. fig 38).

4. *Salmo salvelinus.* Similar to the preceding, but much older. The main bifurcation extends to near the pectoral region. The second bifurcation affects the left component, and only reaches to the optic lobe region (Klaussner, *123* p. 32, Taf. VI. fig. 40).

5. *Salmo fario.* A specimen in which the absorption of the yolk is well advanced. It belongs to the same type as the preceding ones. The main bifurcation reaches behind the pectoral region, a pair of *inner* pectoral fins being present in its angle. The anterior bifurcation affects the right component from the pectoral region forwards. Of the twin heads produced by this latter bifurcation, the right one is reduced and on the way to becoming a parasite on its neighbour (Klaussner, *123* p. 33, Taf. VII. figs. 42-43).

6. *Salmo fario.* Also at a stage well advanced as regards absorption of the yolk. An apparently simultaneous tripartite division takes place just behind the pectoral region. Inner pectoral fins are present in both angles thus produced (Klaussner, *123* p. 34, Taf. VII. figs. 44-45).

The preceding cases all belong to B. 1 of the appended Classification Table (p. 38).

7. *Salmo fario.* A moderately early stage. Two embryos are seen coming together at their extreme posterior ends. The right one bifurcates just behind the region of the medulla. The posterior ends of the two main components diverge in such a manner that one cannot consider them as exhibiting axial union, though probably, had they survived, their tails would have remained united by paraxial structures. Accordingly, the specimen belongs to B. 2 of the Classification Table on p. 38. It is recorded by Klaussner (*123* p. 39, Pl. VI. fig. 39).

8. *Salmo fario.* The specimen described in this paper. The axes of the two defective embryos are united. These last, however, do not undergo true axial union with the principal embryo, being united with the latter only by paraxial structures. The specimen is accordingly to be referred to B. 2 of the table.

9. *Salmo fario.* The verbal description of this specimen (Klaussner, *123* p. 34, Pl. VIII. figs. 46-47) bears out that there are three completely separated embryos, all being smaller than normal, and one very markedly so. However, both of the illustrations seem to indicate union on the part of the tails of two of the embryos. If the description is right, this specimen will belong to Division I. of the Classification Table, and allowing for differences in the general conditions of development, will be in line with those instances among mammals in which three separate embryos are found within the same chorionic sac. On the other hand, if the figures are correct, the specimen will have an important bearing on the question as to how far apart on the blastodermic margin embryonic

rudiments must appear in order that the growing embryonic axes may remain separate along their whole length (see p. 7 and p. 30).

10. *Petromyzon planeri.* The example of caudal triplicity recorded by Barfurth (*8*) in a larval Petromyzon should be referred to here. The larva has three tails, each of which contains a spinal cord, notochord, and caudal artery, as well as muscle plates and skin. Barfurth, however, considers that probably two of the tails originated by a process of supra-regeneration after injury. If this be so, the specimen is not properly referable to B. 1 of the table, which includes examples of true posterior axial triplicity occurring in the mammals alone.

11. *Salmo fario.* Klaussner describes a remarkable instance of anterior quadruplicity. The posterior end is single. The main bifurcation extends to behind the pectoral region, and each of the components is divided as far back as the optic lobe region. The four heads are all defective, being unprovided with eyes (Klaussner, *123* p. 32, Taf. VI. fig. 41).

12. Schmitt (*216* p. 37) mentions the occurrence of several triple forms and of one quadruple form in the set of 900 eggs (*Salmo fario*) referred to on p. 1 as having provided 68 double monsters. Descriptive details are, however, awanting.

MODE OF DEVELOPMENT.

Regarding the mode of growth, and the causation of triple monsters, little can be added to what was said under these headings in the part dealing with double monstrosity (pp. 6-8). All the available evidence goes to show that double and triple forms arise in essentially the same manner, that is, by the appearance of different centres of embryo-formation at a greater or less distance from one another on the margin of the blastoderm. The example (*Instance* 1, above) recorded and illustrated by Lereboullet, and the other early examples noted by Rauber (see Text-figure on this page) and Klaussner leave no room for doubt on this matter. We are speaking here, it will be understood, of anterior duplicity and of union by the yolk-sac only (anadidymus and anakatadidymus), no triple form showing mesodidymus or katadidymus having been put on record. The heads invariably point in one direction, as occurs also in the double monsters, for a precisely similar reason (p. 7).

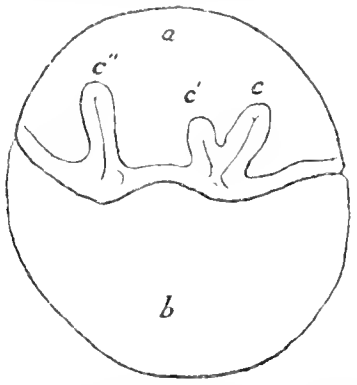


FIG. 5.—After Rauber (*202* 6, Taf. VIII. fig. 14). Egg of trout sixteen days after fertilisation, showing three embryonic rudiments which are slightly unequal in size. Two of these (*c*, *c'*) are already uniting posteriorly, while the third *c''* is some distance apart along the margin of the blastoderm. The specimen is described under (2) (p. 35).

It will be remembered from the part dealing with double monstrosity (p. 7) that two embryonic rudiments which are to remain entirely separate from one another need to arise at a very considerable angular distance (approx. 165°) from one another on the edge of the blastoderm. If the description attached to *Instance* 9 of triple monstrosity in fishes be literally followed, our estimate of the distance in question will have to be reduced at least to 120°. On the other hand, if the illustrations in connection with *Instance* 9 are correct, they supply evidence that the previous estimate was not far from being true.

Triple monster fish showing simultaneous tripartite division are possible forms. *Instance* 6 of the preceding series may have been an example. The mode of formation could be explained by assuming that the two outer centres of embryo formation appeared at an equal distance from the middle one on the edge of the blastoderm. The chances are that this will happen very rarely indeed, while, even when it does happen, there is always the likelihood that the egg as a whole, or one or other of the components, will not survive long enough to give the monstrosity a chance of being observed.

There do not appear to be any records, ancient or modern, indicating survival, or reputed survival, of a triple monster fish beyond the embryonic period. Even as regards that period we still know of examples only from *Esox* and the *Salmonidae*.

TRIPLICITY IN OTHER VERTEBRATES.

Amphibia. Although re-duplication of parts is fairly common in the Amphibia (Gemmill [1]) examples of triple monstrosity appear to be exceedingly rare. The nearest approach to the condition that the author can find occurs in the *Pelobates* larva described by Bruch,[2] in which the axial parts of the tail divide posteriorly into three. This condition, however, as in Barfurth's (8) *Petromyzon* larva, was probably the result of injury.

Reptilia. A very early stage in the ring snake is figured by Wetzel,[3] in which there are three centres of segmentation on the yolk, and one of the centres is itself double. In the older records, a three-headed snake is stated to have been seen at Lake Ontario (Mitchill, quoted from Bruch, as above, p. 172). Then there is also the account reported in Aldrovandi (*2* 427) of a snake with three heads that was killed in the Pyrenees.

The occasional formation, by way of supra-regeneration after injury, of a triple tail rudiment (in Lizards), may also be mentioned here, as under *Amphibia*.

Birds. Examples of triplicity in developing eggs have been recorded by :

Dareste (*53* p. 456, Pl. XIV. fig. 5). Two blastoderms on the same yolk, one with a single embryo, the other with two separate embryos, of which one is smaller than its neighbour and has no heart.

Dareste (as above, but Fig. 4). Three separate embryos on a single blastoderm.

Dareste (as above, but only mentioned in note on p. 456). One area pellucida, with three embryos united by the heads.

Dareste (as above). Two blastoderms united together, one of them with a single embryo, and the other with an embryo having two heads.

Rauber. A common vascular area surrounding two areae pellucidae, one of which is small and bears a single embryo, while the other has two embryos lying close together and uniting by their adjacent body-walls. (*Morph. Jahrb.* Leipzig **5** 167-190 Pls. XII. XIII.)

Moriggia. A single blastoderm carrying three separate embryos. (Quoted from *247* **3** p. 464.)

Koch. An area pellucida carrying two embryos, one of which shows anterior duplicity. (Quoted from *247* **3** p. 465.)

A case recorded by Tur should also be referred to here. I have only access, however, to the very brief description of it given by Windle.[4] "There were four separate centres of development. On three of these there was a primitive groove, and one of these grooves was double."

Mitrophanow also figures a chick blastoderm with several (at least three) primitive streaks. M.'s figure is reproduced by Schwalbe (*222* ii. p. 26).

Mammals. A few examples of unioval triplicity, but none of triple monstrosity, seem to have been recorded since the publication of Taruffi's work on Teratology (*247*). This author very properly emphasises the occurrence of unioval or homologous triplets in the human subject and in other mammals, and refers such cases to an origin similar to that of identical twins, namely, the development of more than one embryo from a single ovum (*247* **3** p. 450-460). More recent instances of this kind are given by (*a*) Walla, (*b*) Breitschneider, and (*c*) Watson.[5]

Of triple monstrosity, Taruffi has collated eight examples in the human subject, four in the dog, and four in the sheep (*247* **3** p. 465 *et seq.*). The accounts of these records need not be reproduced here, and, indeed, the older records are often defective in respect of detail. Some of the cases will be referred to in the notes appended to the following scheme suggested for the classification of examples of Germinal Triplicity.

[1] Supernumerary limb in a Frog, *J. Anat. Physiol.* London, **40** (387-395).

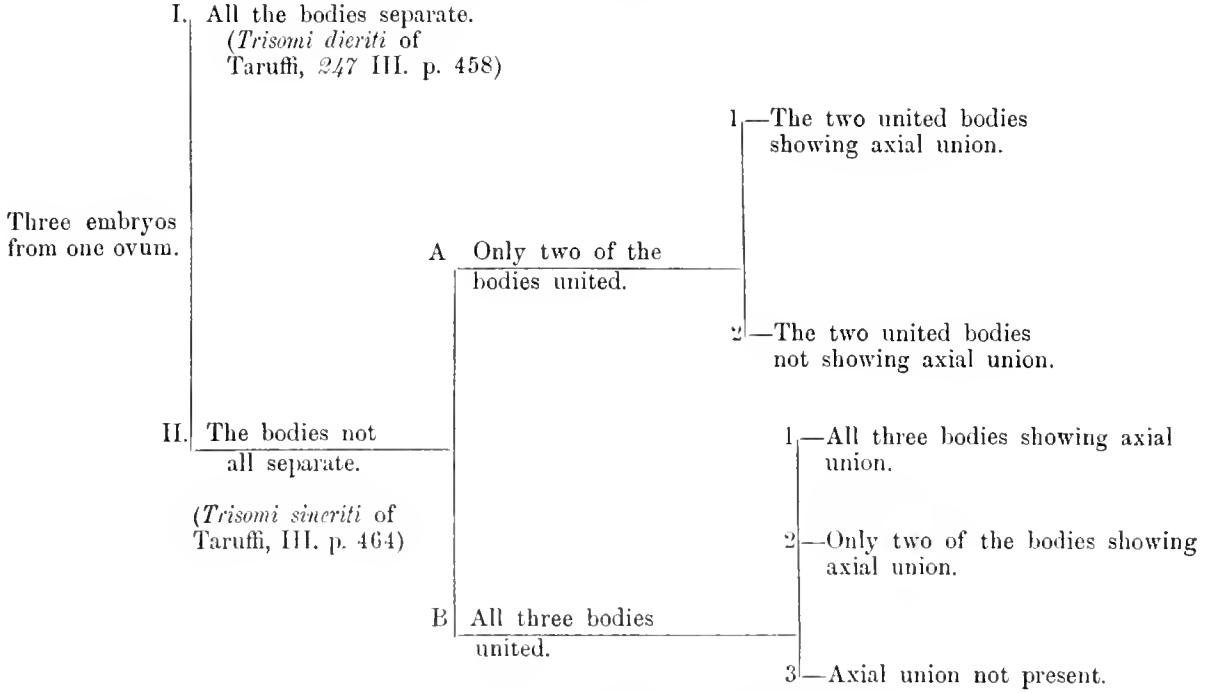
[2] Ueber Dreifachbildungen, *Jenaische Zeitschr. Natw.* **7** (142-175).

[3] Drei abnorm. gebildete Eier von *Tropidonotus natrix*, *Anat. Anz.* Jena, **18** (425-440).

[4] Report on Teratological Literature, *J. Anat. Physiol.* London, **40** p. 296.

[5] (*a*) and (*b*). Quoted from Windle's Reports in *J. Anat. Physiol.* London, **37** p. 302, and **38** p. 365. (*c*) *British Medical Journal*, Jan. 9, **1904** p. 75.

CLASSIFICATION IN GERMINAL TRIPLICITY.



The divisions A. 1, B. 1, and B. 2 may be further subdivided according as the union of the bodies is anterior or posterior (anadidymus and katadidymus).

A single condition of the neural axis and the axial skeleton, at least for some part of their length, should be taken as their criterion of axial union.

Notes to the Classification Table. Under I. will be included the cases of identical triplets already referred to. These are probably much less rare (*247* III. p. 460, 19, 20) in the human subject than are cases of triple monstrosity. Instances of quadruple, and even of quintuple, pregnancies with single chorion and placenta, and presumably of unioval origin, have also been recorded (*247* III. p. 459).

The remarkable observation by Assheton (*J. Anat. Physiol.* London, **32** 362) of two germinal areas on a single blastocyst of the sheep, threw very striking light on the probable mode of origin of identical plural embryos. Still more remarkable is the recent work of Fernandez[1] on the embryology of the Edentate *Tatusia hybrida* Desm. Confirming and greatly extending previous observations by v. Kölliker, Milne Edwards and v. Jhering, this author finds that normally in *Tatusia* all the eight or nine foetuses in a pregnancy arise from a single ovum, are unisexual, and are enclosed within the same chorionic sac.

In the lower vertebrates, the mode of development does not, in the end, allow so complete a separation of the embryonic bodies as is possible in the mammals. Taruffi, however, points out with justice that, in the chick, such examples as the second quoted from Dareste, and that described by Moriggia, are similar in their essentials to his mammalian trisomi. So also is the triple salmon of Klaussner, according to the description stating that the three embryonic bodies were quite separate except for their attachment to the common yolk-sac.

A. 1. Examples are the fourth of the chick embryos noted above as described by Dareste and that described by Koch.

A. 2. Had it survived, the first of the chick specimens from Dareste would have come to

[1] Beiträge zur Embryologie der Gurtelthiere, I. *Morph. Jahrb.* Leipzig, **39** Heft 2.

be of this type through inclusion of the smaller acardiac embryo in the body-wall of its more vigorous neighbour.

B. 1. This is the commonest kind of triple monster in the fish. See cases 2, 4, 5, 6, p. 35. The type usually exhibits bifureation of one of the branches of an already divided axis, but it seems possible that simultaneous tripartite division may have been present in case 6 of the fish series, and perhaps also in some of the three-headed monsters recorded by older authors, to which reference is made in Taruffi (*247* III. 466 *et seq.*; Oss. 4, 5, 6, 7, 9, 12, 14). However, very careful dissection will be required before tripartite division is definitely shown to have occurred. In the case of the fish embryo, the examination would need to be done by serial sections.

The triplicity in the cases just mentioned is anterior, but posterior axial triplicity seems also to occur in mammals (*247* III. p. 471; Oss. 15, 16, 17).

B. 2. Specimens 7 and 8 of the fish series belong to this subdivision, which also includes what may be called the classical instance in the human subject, viz. that described by Reina.[1]

B. 3. Examples are recorded by von Froriep[2] in the sheep, and by Fiedler[3] and Bettoli and Fattori[4] in the human subject.

[1] *Atti dell. Accad. Gioen.* 8 p. 203.
[2] Gurlt's *Lehrbuch der Pathologischen Anatomie*, II. p. 201, Berlin 1832.
[3] Quoted from *247* III. p. 465.
[4] Quoted from Bruch, *Jenaische Zeitschr. Natw.* 7 p. 158.

CHAPTER III.

CYCLOPIA.

Pl. XXIV. fig. 100 (external appearance, see also Pls. I. fig. 3 and II. fig. 11); XXIV. figs. 101-104 (various structures); XXV. figs. 107-108 (sections of head), and figs. 109-110 (semicyclopia).

Classification and structure, - - - - - - - - - - p. 40
Summary and comparison, - - - - - - - - - - - p. 42
Other records in fishes, - - - - - - - - - - - p. 43
Causation, - - - - - - - - - - - - - p. 44

Cyclopia rarely manifests itself in developing trout eggs. Under ordinary fish-hatchery conditions it may be put down as being ten or fifteen times less frequent than double monstrosity. Altogether I have obtained only six examples. It is noteworthy that two of these were provided by double monsters in which one or other of the twin heads showed the defect in question (Pl. I. fig. 11, cf. I. fig. 3).

The total number of specimens is hardly large enough for systematic purposes, but I find that here, as in the first groups of double monsters, the condition of the nervous system affords a basis for classification into at least two main divisions. The first (A) is characterised by fusion, more or less complete, of the cerebral lobes (two specimens); while the second (B), in addition to fusion of the cerebral lobes exhibits fusion on the part of certain structures belonging to the third ventricle and the mid-brain regions (three specimens). The sixth specimen was not cut into serial sections, and accordingly I cannot say for certain to which division it belongs. In view of the probable causation of cyclopia (p. 44) it will be understood that while the condition is always associated with cerebral defects, these defects need not be of a perfectly uniform character, nor need the fusion or reduction of the two eyes always correspond in amount with the fusion or reduction present in the two sides of the brain.

(A) *Cyclopia with Fusion of the Cerebral Lobes (two specimens).*

The external appearance is illustrated by Pl. XXIV. fig. 100. The front of the head is wedge-shaped, its size being reduced in the transverse and increased in the vertical line. The large median eye is overarched by a mesial frontal process carrying a pair of small closely approximated olfactory pits (Fig. 101). Upper and lower jaw arches are present. The posterior part of the head and the body are normal.

Cranial Skeleton. The skeleton is greatly modified in front of the pituitary region. The trabeculae cranii pass downwards so as to lie below the median eye. They are widely separated from the base of the brain and they take no part in the formation of an olfactory capsular cartilage. Anteriorly, they articulate with short palato-quadrate bars. In the normal Trout embryo at a corresponding stage, the trabeculae, though united, still show evidence of their double origin. But in all my cyclopic specimens the trabeculae form an absolutely single piece right back to the pituitary space.

A rudimentary olfactory capsule is derived from the united anterior ends of the supra-orbital bars. This united portion lies in the frontal process and is perforated by the two small olfactory

nerves. Posteriorly, the supra-orbital bars separate and pass along the dorso-lateral aspects of the brain to join the auditory cartilages, as in the normal condition. Near their place of separation, each gives origin to an obliquus oculi superior muscle.

The mandibular, hyoid, and palato-quadrate bars are appreciably shortened in accordance with the small transverse measurement of the mouth.

Brain. The cerebral lobes are slightly smaller than normal, and are in great part united along their inner faces. The median longitudinal fissure penetrates for only a third of their depth in front at the place of origin of the olfactory nerves, while posteriorly, close to the third ventricle, the fissure in question appears simply as a shallow groove. The third ventricle region and the optic lobes are well developed, pineal diverticulum, optic recess, hypophysis, and hypoaria being present as in the normal condition. A transverse section at the origin of the olfactory nerves shows an area of brain which is ·66 of normal size as judged from a specimen of the same age. The proportion to normal in a similar section at the back part of the cerebral lobes is ·95, while the middle region of the optic lobes shows a sectional brain-area which is slightly in excess of normal.

There is no dropsy of the central cavity of the brain or of the meninges. The cranial nerves are all present and are normal, with the exception of the first two pairs, the olfactory nerves being small and closely approximated, while the optic tracts unite at the commissure to form a single optic nerve.

Eye. The globe is large and has its transverse diameter increased, as also has the lens. The lens-cavity is not completely occupied by fibres, a space being left anteriorly which is filled by small round cells. Retina, choroid, cornea, vitreous humour, and sclerotic are well developed. The single choroidal fissure leads back to a large optic nerve formed, as above stated, by the union of the two optic tracts. There are two choroidal glands, one on either side of the optic pore. They are supplied, as usual, by choroidal arteries coming from the pseudobranchs. The following eye-muscles are present: two superior obliqui, arising from the supra-orbital bars; two superior recti, arising along with two inferior recti from the fibrous capsule of the brain in front of the hypophysis; two external recti, which are normal in origin and are inserted into the right and left sides respectively of the eyeball. The inferior recti are united close to their insertion into the eyeball. Inferior obliqui and internal recti are absent.

(B) *Cyclopia with Fusion of the Cerebral Lobes and of Structures in the Mid-brain.*

Three of my specimens exhibit this condition, two of them possessing a single median eye, while the third, although showing the other essential features of cyclopia, has a pair of small closely-approximated eyes.

1. The specimens which have a single eye resemble type (A) in general appearance, except as regards their mouth-parts. In place of the upper jaw there is a membranous flap on either side projecting downwards and forwards from below the eye. In place of the lower jaw arcade there is a narrow mesial process projecting forwards to end just between the flaps. Microscopic examination of the flaps shows that they contain externally a number of young teeth and internally a commencing membranous ossification. They are probably to be compared with un-united maxillary processes, while in appearance they resemble the horn-like structures found by Paolucci (*181*) in his cyclopic ray.

The mesial process above mentioned contains a much elongated symphysis of the lower jaw, the Meckel's bars of which diverge little from one another and articulate with suspensoria which are similarly approximated.

Skeleton. The trabeculae cranii are represented by a single exceedingly short bar projecting downwards and forwards towards the wall of the pharynx. Quite separate from this are the palato-quadrates, the anterior ends of which, uniting below the eye, form a mesial plate replacing the defective trabeculae. The supra-orbitals are different in the two specimens: in one, they unite anteriorly in the frontal process, giving rise to a small olfactory capsule; in the other, they are short and extend no further forward than the middle of the fore-brain. In this latter case, the olfactory

region is destitute of cartilage and there is no tegmen over the third ventricle. In both specimens the supra-orbitals are displaced downwards so as to be ventro-lateral to the brain. The auditory cartilages are displaced similarly but in a slighter degree.

Brain. The cerebral lobes are markedly reduced in size and are fused together, the longitudinal fissure being almost entirely absent. The central cavity is slightly enlarged and extends downwards on the outer sides of the lobes further than in the normal condition. The pineal diverticulum is a small unstalked pouch. The optic lobes are of considerable size and are normal as regards their dorsal parts, but internally the mesial furrow of the central canal is only slightly marked, and there is absence alike of the optic recess, of the hypophysis, and of the hypoaria. Optic tracts and nerves are absent. As in type (A), the olfactory nerves are small and closely approximated.

A transverse section at the origin of the olfactory nerves shows an area of brain which is only ·32 of normal size as judged from a specimen of the same age. The proportion to normal in a similar section at the back part of the cerebral lobes is ·7, while the middle region of the optic lobes is very distinctly (1·3 times) in excess of normal. Compare with the corresponding figures for the (A) type of cyclops.

Eye. The single small deeply embedded eyeball has no choroidal fissure, vitreous humour, or optic nerve. The lens and the retina are, however, fairly well developed and there are two choroidal glands. The position of the optic pore is marked inside the eyeball by an interruption of the retina exhibiting a few nerve-fibres, which fail to pierce the hexagonal pigment layer or the sclerotic (Pl. XXIV. fig. 104). Two external and two superior recti muscles are present. The other eye-muscles are awanting, with the exception of a pair of small superior obliques occurring in the specimen mentioned as having its supra-orbital bars extending forward into the frontal process.

Mouth. The mouth-opening is represented by a minute canal, beginning at the bottom of the groove between the maxillary flaps and extending backwards above the symphysis of the lower jaw. In one case this canal ends blindly, in another it joins the pharynx.

2. The specimen which had two small eyes closely approximated but un-united shows the following characters: cerebral lobes well developed, deeply cleft anteriorly, but united posteriorly; pineal diverticulum small; third ventricle almost obliterated; incomplete fusion of structures in the floor of the optic lobes; rudimentary hypophysis and hypoaria; optic tracts and nerves absent; eyes small, embedded, almost touching one another, without choroidal fissure, vitreous humour, or optic nerve, but with well-developed lens, retina, and retinal pigment-layer; superior obliqui as well as superior and external recti present for each eye; inferior recti and obliqui wanting; no mouth, the upper and lower jaws being sealed together; trabeculae cranii extremely short, forming a single bar projecting downwards and forwards into wall of pharynx; olfactory capsules absent; supra-orbital bars ending separately in front, the tip of each giving origin to an obliquus oculi superior; olfactory pits approximated and supplied by small olfactory nerves.

Summary. Olfactory Organs.—Olfactory nerves and pits, reduced in size, are present in all my specimens. The olfactory pits lie close together on the inferior aspect of the mesial frontal process.

Brain.—Fusion of the posterior parts of the cerebral lobes is found in all my specimens. By itself, as in type A, this condition is compatible with the presence of a well-developed cyclopic eye possessing vitreous humour and an optic nerve, as well as with the presence of pineal diverticulum, hypophysis, and hypoaria, and of optic tracts and optic recess.

Fusion of the basal structures in the mid-brain, as in type B, is associated with greater defects, viz. reduction in the size of the eye-ball; absence of choroidal fissure, optic nerve and optic tracts; absence or rudimentary condition of hypophysis and hypoaria.

The absence of dropsy of the central cavity of the brain is remarkable.

Eye.—As seen in type A, the eye may be remarkably well-developed, possessing lens, retina, vitreous humour, retinal pigment, and optic nerve. A double set of normal eye-muscles, excepting only the internal recti, may be present. Paired superior and external recti are constant, while the superior obliqui and the inferior recti are variable. The remarkable set of conditions which

accompanies fusion of mid-brain structures has been mentioned above in connection with the brain.

Skeleton.—The trabeculae cranii appear as a single bar of cartilage underlying the median eye. Either they formed a single structure from the first, and this seems to me most probable, or their fusion was remarkably early and complete. Olfactory capsular cartilages may be present or absent; when present, they are developed in connection with the anterior ends of the supra-orbital bars. The palato-quadrate, the mandibular, and the hyoid bars tend to be shortened, in correspondence with the general transverse narrowing of the mouth-parts.

Comparison with Cyclopia in Mammals. 1. While olfactory nerves are not found in the typical mammalian cyclops, they are present in all my trout specimens, being traceable from the fore-brain to the small olfactory pits on the under surface of the frontal process. If, as seems certain, this process represents the "proboscis" of a cyclopic mammal, the "proboscis" in question can have no relation with parts of the brain behind the cerebral lobes, and, in particular, none with the hypophysis.

2. Dropsy of the central cavity of the brain or of the space between brain and skull is not characteristic of cyclopia in fishes. This may be contrasted with the usually dropsical condition of the hemispheres and the meninges in cyclopic mammals.

3. The relatively good development of all parts of the brain, particularly in type A among fishes, is remarkable. Indeed, there seems to be no absolute bar to prevent a specimen of this kind from surviving and obtaining food for itself as in the remarkable case recorded by Paolucci.

Other Records in Fishes. The literature of cyclopia in fishes is by no means extensive. Small as it is, however, it provides two most interesting facts. One has reference to the growth and survival of a cyclopic fish, and the other to an agent in the production of cyclopia, which seems almost specific in its action.

Lereboullet (*143*) figures a pike embryo with a cyclopic eye which is furnished with a single lens, and has probably arisen by the fusion at an early stage of two separate eye rudiments. Girdwoyn (*81*) also figures a typical cyclopic salmonid embryo well advanced in development, and resembling the specimen I have illustrated in Pl. XXIV. fig. 100.

The remarkable instance of survival referred to above was recorded by Paolucci (*181*). The specimen, caught in the Adriatic not far from shore, and placed in the Natural History Collection of the Technical Institute at Ancona, was identified by F. Paolucci as probably belonging to the species *Myliobatis noctula* Dum., though it presented certain characters intermediate between this species and *Myliobatis aquila*. The dimensions, as judged from the author's illustrations, are: length of head and body, not including the tail, 9½ inches; breadth between tips of pectoral fins 17 inches. There is a single very large median eye, set in the place of what should be the fleshy anterior border of the head. This border is divided into two parts sticking out like horns, "3 cm. long, and as thick as a finger," one on either side of the eye. The nostrils and the fleshy upper lip are both awanting. The above record, regarding the authenticity of which there seems not the slightest reason to express doubt, is probably the only one which indicates that any vertebrate animal has ever been found in actual adult life embodying the fabled Cyclops type.

A very interesting set of experiments has been carried out by Stockard (*237*) on the production of cyclopia in the eggs of *Fundulus heteroclitus* by the addition of magnesium chloride to the sea-water in which the eggs were being hatched. With certain strengths of solutions (⅓ m. sea-water solutions of $MgCl_2$), one-eyed embryos occurred with surprising regularity in 50% of the eggs. The remaining embryos in these solutions were apparently normal so far as the eyes were concerned. The structure of the compound eye corresponded almost exactly with that described above under cyclopia (A). Stockard does not give particulars regarding the brain, but from his figures, particularly Figs. 4-5 p. 253, it may be inferred that some degree of fusion existed in the region of the cerebral lobes and the third ventricle. As regards the coming together of the two eyes, Stockard considered it to be through an antero-medio-ventral fusion of the elements of the two optic vesicles at an early developmental

stage, this fusion being more or less complete in the different embryos. He thought it probable that the resulting large optic cup induced the formation of a single lens, the lens being formed of ectoderm different in position from that of the normal lens-forming cells. He adds that probably there is no localisation of lens-forming substance in the ectoderm of the fish embryo, and that it is the underlying optic cup which induces actual lens formation on the part of the ectoderm. This is more or less in harmony with the result of recent experimental work on the development of the amphibian eye. On the other hand, it would render difficult of explanation those cases of defective heads in embryo fish which possess one or more lenses without any trace of corresponding optic cups.

Semicyclopia and allied conditions. Alike in single embryos and in double monsters, one may come across examples in which the heads show lateral compression. In extreme instances, the whole anterior part of the head may be atrophied, the mouth being deficient, the brain profoundly malformed, and the eyes absent or represented only by the lens. (See Pl. XXV. fig. 106, XXVII. fig. 112.) When the defective condition is moderate in degree, the eyes and the olfactory pits are brought together, the mouth narrowed, and the trabeculae cranii ventrally displaced, so that they lie below the approximated eyes and fail to join the olfactory cartilage in front. This condition, which may be called semi-cyclopia, is illustrated in Pl. I. fig. 3 and XXVI. figs. 109, 110. Similar specimens are figured by Girdwoyn (*81* p. 112) and by De Quatrefages (*198* Pl. VII. fig. 2). See also p. 51.

Causation. 1. It seems probable that the causes which produce cyclopia in fishes are sometimes purely mechanical, and that under favourable circumstances they may exercise a minimal degree of interference with the development of other structures, in particular with that of the brain. Under ordinary circumstances, and apart from such experiments as those of Stockard, pressure, or at any rate want of space for development, may be put down as the commonest causal factor. The egg-membrane of the trout is tough and strong, while the cavities of the optic bulb and stalk, and even that of the central nervous system, are developed secondarily in solid masses of cells. It may be supposed that undue lateral pressure, from whatever cause (*e.g.* partial coagulation of the yolk, swelling due to differences of osmotic pressure, want of space from twinning of the head), may bring the optic buds together and cause them to unite *during their actual outgrowth*. If only moderate in degree this pressure might next allow a central cavity to form in the single bulb and stalk. Such a central cavity would permit the development of the secondary optic vesicle with its choroidal fissure. The choroidal fissure would enable mesenchymal cells to pass into the interior of the eyeball and form a vitreous body, and would enable also nerve-fibres growing from the retina to escape from the eyeball, pass along the optic stalk, and form an optic nerve and tracts such as are actually found in type A. The effect of moderate pressure on the brain may perhaps be recognised in the fusion of the posterior parts of the cerebral lobes characteristic of this same type.

A greater amount of lateral pressure might lead to such further degrees of fusion affecting the third ventricle and the mid-brain as are illustrated in type B. In the eye it may greatly hinder the formation of a central cavity in the primary optic vesicle and stalk. This might prevent the formation of a choroidal fissure by the usual method of ventral cupping. In the absence of a choroidal fissure, mesenchyme could not enter behind the lens to form a vitreous humour, and nerve-fibres formed in the retina would have no exit from eyeball to stalk, and the stalk itself would degenerate. The condition in type B might then be realised, *i.e.* an eye, reduced in size, without choroidal fissure, vitreous humour, or optic nerve.

2. The apparently specific action of magnesium chloride in producing cyclopia is at present impossible of explanation if, as Stockard seems to have proved, it does not depend on differences of osmotic pressure. Stockard (*237*), however, points out that probably other substances are capable of exercising other specific effects on developing eggs, and calls attention to the characteristic Lithium larvae of Herbst, to Morgan's frog larvae and to his own fish embryos.

3. Although positive evidence is awanting, I think it extremely likely that cyclopia may sometimes have a spontaneous or autogenetic origin. In this respect it would resemble various

other abnormalities which are also capable of being produced by the action of external factors, and do not depend directly on atavism. The remarkably perfect and symmetrical nature of the anatomical adjustments that is sometimes found both in the eye itself and in the surrounding parts, seems to point to this conclusion. According to the view already expressed (pp. ix-x), the fact that cyclopia may be produced by environmental factors, is rather an argument for, and not against, the probability that it may also arise by abrupt spontaneous variation.

CHAPTER IV.

MINOR ABNORMALITIES.[1]

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HERMAPHRODITISM.

UNDER this heading we have to deal almost entirely with *true* hermaphroditism, since the Teleosts (which provide the vast majority of instances) do not, on the whole, possess accessory genital structures which are peculiar to either sex. Among other fishes, the only instance of *spurious* hermaphroditism I have come across is provided by the adult male skate described by Matthews (*151*) as possessing an oviduct on the left side. The specimen measured over two feet in length and had practically perfect glands and ducts of the male type on either side. In addition there was a Müllerian duct of full adult size on the left side. This duct was furnished with a large oviducal gland and contained numerous living spermatozoa in its anterior (Fallopian tube) portion. It may be noted in this connection that the male *Raia clavata* is occasionally found with teeth as much blunted as those of the female (Day *54* II. p. 344).

True hermaphroditism, normal. As is well known, the condition occurs normally in a number of fishes. Following Howes (*101*) with slight modification, we may distinguish three types of

[1] The following paragraph from Stoddart (*239* p. 75) is worth quoting at this stage. It shows the frequency with which abnormalities of many kinds occurred in trout from Scottish waters before artificial hatching was practised, and at a time when the amount of sewage pollution must have been vastly less than it is now.

"We have caught them hump-backed and covered with sores, blind of one eye, wanting a gill or a fin and crooked up in all shapes. On the Tay we once took an individual with a short round upper head like that of the bull-dog and the lower lip projecting beyond it. We understand that a variety of this kind is to be found in Loch Dow in Inverness-shire. On the Water of Leith we saw a friend capture three successively out of one stream all of which wanted the tail; this defect was most probably occasioned in winter, the water from which they were taken happening to be extremely shallow and the frost before being somewhat severe."

the condition: (1) successive unicyclic (*monocyclic* Masterman *150*); (2) successive multicyclic (*polycyclic* Masterman); and (3) synchronous. To the first group belong those fish which, like *Myxine*, ripen only sperm when young and afterwards only eggs; to the second, those which are protandrous in each season; and to the third, those in which the ripening of both kinds of sexual products takes place at much the same time in each period of breeding.

True hermaphroditism, abnormal. A very large number of instances have been recorded, chiefly from the Teleosts. References to the more important of these will be found under the following index numbers.

Fuhrmann *71*; Halbertsma *89*; Hefford *90*; Howes *101*; Iwanzoff *105*; Jäckel *107*; Järvi *113*; Johnstone *118*; Kyle *135*; Lowne *146*, pp. 164-5; Luther *147*; Martens, *149*; Masterman *150*; Newman *167*; Orlandi *177*; Patterson *184*; Poey *193*; Sandman *214*; Schneider *218-9*; Simpson *226a*; Smith *228-30*; Smitt *231*; Southwell *232*; Stewart *235*; Vogt *265*; Weber *268*; Williamson *269-270*.

The limits of this work make short treatment of the present subject necessary, but certain of the papers named above may readily be consulted for supplementary details. In particular, Weber gives a valuable résumé of what was known on the subject up till 1884. Howes adds some cases, and also initiates a very interesting discussion on the general questions involved. Stewart contributes the solitary well-described instance in the *Salmonidae*, and an interesting example in the mackerel. Masterman adds two cases, and continues the discussion begun by Howes. More recently five other instances have been supplied by Williamson (*269-270*). Abnormal hermaphroditism has now been recorded in examples of the *Percidae, Squamipinnes, Sparidae, Scombridae, Mugilidae, Gasterosteidae, Labridae, Gadidae, Pleuronectidae, Cyprinidae, Esocidae, Salmonidae, Clupeidae.* The condition seems also to have been recorded in *Acipenser*, and among the *Selachii* (see Howes *101*, p. 543).

Classification. Decisive evidence is not easy to obtain, but I believe that, on the whole, abnormal hermaphroditism in Teleosts belongs to the third or synchronous type. The cases recorded by Stewart (*235*) in the trout and mackerel were marked by the presence at the same time of fully developed ova and sperm. No doubt various other recorded examples have shown apparent protandry, and this circumstance, together with the fact that normally the females are larger than the males, has led some authors to consider abnormal teleostean hermaphroditism as belonging to the successive polycyclic type. It must be noted, however, in the case of many dioecious animals, that during each season motile sperm is present abundantly in the testis of the male, months before the contents of the ovary are fully ripe (*e.g.* sea-urchin, limpet, and other mollusca). The argument regarding size is hardly relevant to cases in which the sexes are united.

Structure. It will be remembered that in the majority of osseous fishes the ovaries are paired, and that the ova when ripe dehisce into their central cavities, which unite posteriorly in a single efferent duct. In the males also, the efferent channels, though frequently different in form, are built essentially on the same plan. The *Salmonidae, Muraenidae, Cobitis*, and some others, are exceptional in that the ova when ripe dehisce into the body cavity, from which they escape by means of oviducal pores. In such fish, however, the males exhibit the typical arrangement as regards their efferent ducts.

In hermaphroditic conditions, very great differences in the relations of the two kinds of tissue occur. For example:

(1) One or more masses of spermatic tissue may be contained in, or attached to, some part of one or both of the ovaries. In such cases the testicular ducts open into the cavity of the main gland and are thereby placed in communication with the exterior. Or, *mutatis mutandis*, the converse conditions may occur. The vast majority of the instances may be grouped in this division.

(2) The gonad on one side may be entirely male and that on the other entirely female. The gonads unite posteriorly just as two ovaries or two testes do, and their ripe products escape by one genital aperture (cf. Williamson *269*).

(3) There may be an ovary as well as a testis on one or both sides of the body. In the almost

symmetrical instance recorded by Stewart (*235*) from the mackerel, the two testes lay dorsally to the ovaries. Judging from the figures, all four glands opened posteriorly into a single efferent duct.

(4) In the Salmonidae hermaphroditism appears to be exceedingly rare. Its occurrence is mentioned by Simpson (Todd's *Cyclopaedia of Anatomy and Physiology*, London 1836-9, II. p. 697), but otherwise the only example I have come across is that described by Stewart (*235*) from preserved material in the trout. This case merits separate mention, on account of the differences occurring normally between the sexes in the Salmonidae, and also because, on other grounds, it presents features of very great interest. The right genital gland is ovarian in structure. The left, which is the larger, consists chiefly of ovary, but has a middle portion with the structure of a testis. There are two genital ducts, one on either side, leading from the posterior ends of the gonads to the uro-genital chamber. The specimen was therefore regarded as being a fundamentally male fish possessing also partly the female character. The previous history bore out that on two occasions ripe eggs had been extruded from its belly by artificial pressure, and these eggs, although kept completely isolated, developed normal young.

At the time of examination several ova were lodged in the right duct close to its termination in the uro-genital chamber. A short distance in front of this point the duct in question was ruptured or defective. There were between two or three dozen loose ova in the body cavity, but these had apparently escaped from a rupture of the right ovary or from the opening in the wall of the right duct alluded to above.

Nothing in the description indicates the presence of oviducal pores leading from the body cavity into the uro-genital chamber, and presumably in this case the ova dehisced into the interior of the gland and not into the body cavity.

The frequency with which hermaphroditism appears in fishes, normally or abnormally, and the fact that the *Ascidia* are hermaphrodite, have been taken as evidence that the chordate ancestor was monoecious (Haeckel, Howes, Masterman and others). It does not appear that the conclusion is necessary on either ground, any more than that the alternation of generations found in many widely different animals is due to common ancestry, or that the hermaphroditism of the Cirripedes indicates a primitive monoecious condition in the crustacean stock. I believe that here we have an instance (see p. 5) in which a certain "potentiality" (*i.e.* hermaphroditism on the one hand or unisexuality on the other) has become fixed as normal in certain forms (*e.g.* hermaphroditism in *Ascidia*, *Myxine*, *Serranus*, etc.; unisexuality in *Amphioxus* and most fishes), while in these forms the converse potentiality still manifests itself in a sporadic and "teratological" manner, through some inherent variation tendency the persistence and strength of which are independent of atavism.

This view, while not directly supporting Pilseneer's[1] position that the hermaphroditic is always derived from the unisexual condition, points to a property inherent in animal life whereby either state may conceivably receive the opportunity of gradually replacing the converse one through the ordinary working of natural selection.

II.

SHORTENING AND CURVATURE OF THE SNOUT.

(Pug-head; Bulldog-head, etc.)

REFERENCES:

Salmonidae.—Carlet *36*; Couch *45*; Day *54* II. p. 102; Lidth de Jeude *114*; Lowne *146* p. 55; Malloch *147a*; Saint Hilaire *213* I. pp. 283-287; Stoddart *239*; Tornier *250*; v. Krauss *134*.

Specimens have been sent to the author by Henry Lamond, Esq. (*Salmo fario*), and Peter M'Nair, Esq. (*Salmo salar*). As regards early stages, Girdwoyn *81* fig. 112, illustrates a trout embryo with shortened upper jaw and defective also as regards the eyes. A somewhat similar specimen is figured by de Quatrefages (*198*, Pl. VII. Fig. 2).

[1] "Hermaphroditism in Mollusca," *Q.J. Microsc. Society*, London, **37** (19-46).

Other Fishes:

Examples in *Cyprinus* are furnished by Knauthe (*125-6*), Lowne (*146* p. 55), Otto (*178* thirteen instances), St. Hilaire (*213* Pl. I. figs. 4-6), Tornier (*250*); in *Abramis vimba* by Leonhardt (*140*); in *Esox* by Otto (*178*), and Vrolik (*266*); in *Anguilla* by Lowne (*146* p. 55), and Tornier (*250*); in *Lampenus* by Pappenheim (*183*); in *Perca* by Pellegrin (*189*); *in Mugil chelo, M. capito, Gobius ophiocephalus, Labrax lupus, Gadus minutus, Pleuronectes italicus, Merluccius vulgaris,* by Ninni (*168*); in *Cottus* by Nyström (*174*), and in *Mugil capito* by Canestrini (*35*). Leonhardt (*140*) refers to records in *Cyprinus* by Neydeck, Steindachner, and Hofer; in *Lumpenus lampetraeformis, Gadus merlangus, G. morrhua,* and an eel, by Lönneberg; and in *Salmo irideus* and *Esox lucius* by Hofer. Freund (*70*) gives a record, having reference to *Phoxinus laevis.*

In typical examples the snout is markedly reduced in size, and curved in such a way that the anterior frontal region arches rapidly downwards just in front of the eyes. The latter are lessened in horizontal diameter and become oval in shape, having the long axis vertical. The lower jaw retains its usual size, and accordingly projects a considerable distance in front of the rest of the head. The incurving of the tip of the snout may be so great that what should be its dorsal surface comes to look downwards into the floor of the mouth. The deformity varies greatly in amount in different specimens, and also passes without very abrupt separation into the "round-head" condition to be afterwards described (p. 50).

Skeleton. The skull is practically normal as far forward as the anterior border of the eyes. In front of this region the usual skeletal elements tend to occur, but they are reduced in size, altered in shape, and curved downwards, while still retaining as far as possible their ordinary connections with one another. In the region affected, the axial stem of the skull consists of vomer and parasphenoid. Sometimes the stem suffers simple shortening, below and in front of the eyes, and sometimes, in addition to being shortened, it becomes sharply bent on itself in this region, so as to form a V, the apex of which points upwards. These two varieties are connected by intermediate forms.

The frontals curve downwards so that the mesethmoid lies below instead of anterior to them; the lateral ethmoids and the nasals are similarly displaced, while the premaxillaries are so far curved round that they lie behind instead of anterior to the mesethmoid.

The intermaxillary and maxillary are smaller, and carry fewer teeth, than in the normal condition. Thus the former has two teeth in the instance described by Tornier (*250*), and four in that described by Lidth de Jeude (*114*), the normal number being about six. In an excellent example from the eel, Tornier (*250* p. 307) notes that neither the pterygoids nor the maxillaries nor the vomer are provided with teeth, while all these bones have many rows of teeth in the normal condition. The shortened maxillaries lie transversely, or, in extreme cases, are directed backwards. The skeletal elements which go to form the anterior or palato-pterygoid limb of the suspensorial arch are smaller than normal, particularly those near the ethmo-palatine extremity of the limb, where, indeed, some of them may be no longer recognisable. On the other hand, those which form the posterior (hyomandibular-quadrate) limb of the arch in question tend to be of normal size.

A number of these points are brought out in the following description from Carlet (*36 Salmo*). The frontals curve downwards at the level of their orbital processes. The mesethmoid lies below the frontals. The lateral ethmoids and the openings of the nostrils are also displaced downwards. The pterygo-palatine is reduced in length, but the shortening affects the ento- and ecto-pterygoids less than the palatines, which are short and almost transverse. The vomer is slightly shortened, and the parasphenoid is very short, especially in its anterior part. The orbito- and ali-sphenoids are similarly reduced in length. The descriptions by Hofer (*96a*) and Freund (*70*) may also be consulted.

Leonhardt (*140*) gives a careful series of measurements of different parts of the head in his *Abramis vimba* specimens, together with a fairly complete account of their osteology.

Mention should be made of an example from the eel in the Royal College of Surgeons' Museum (Lowne *146* p. 55). The mandibular extends forwards beyond the anterior extremity

of the truncated skull. As regards the brain, "the four anterior ganglia are much compressed from before backwards. The anterior pair of ganglia (olfactory) have displaced the second pair, and lie practically between, instead of entirely in front of, them."

Causation. In the main, the defect seems to be a developmental one of germinal origin, and not acquired through later injury. However, in the Salmonidae, apart from the instances figured by Girdwoyn (*81*) and de Quatrefages (*198*), the occurrence of pug-headed *embryos* does not seem to have been actually put on record.

It is always possible that, as in cyclopia, the defect may at times be due to pressure on the embryo (Leonhardt) or some other factor depending on environment. Tornier (*249*) attempts to show that the condition in question, as well as the other striking variations found in different goldfish races, are due to interference with development through swelling up of yolk elements by undue inhibition of water. This may conceivably explain the occurrence of isolated and irregular instances, but cannot possibly account for the strictly hereditary qualities which the condition has been stated to exhibit.

Knauthe (*125-126*) allowed breeding between a male and female *Leucaspius delineatus* v. Sieb. which, though apparently normal, were derived from "puggy" parents, with the result that thirty out of 250 in the offspring resembled their grandparents (*i.e.* a proportion of 12·5 %). A second brood from the same parents only gave a proportion of 8 %.

Another male and female of *Leucaspius*, normal themselves though derived from "puggy" parents, provided in the offspring the large number of fifty out of 180 which "reverted" to the grandparental form.

The same author, experimenting with a different species (*Cyprinus aphya?*), obtained breeding between two pairs of males and females, apparently normal and derived from apparently normal parents, but having "puggy" grandparents. The result was that twenty out of a total of 210 in the offspring resembled their great-grandparents.

In the succeeding year Knauthe was able to obtain breeding between some of the seemingly normal examples of the latest generation noted above. Six of the progeny out of a total of 168 were "puggy," that is to say, resembled their great-great-grandparents, and yet, as has been detailed above, the intervening ancestors were all apparently normal. A control brood in a kindred species of similar age reared under exactly the same conditions provided not a single example of "pugginess." The repetition and extension of Knauthe's experiments are greatly to be desired.

THE ROUND-HEADED CONDITION.

The skull is more or less sharply humped upwards in the frontal region so as to present a somewhat prominent brow, or forehead. The eyes are compressed antero-posteriorly, forming ovals with the long axis vertical. The anterior part of the snout is not ventrally incurved, nor does the lower jaw project markedly beyond the upper one. Tornier (*250*) seems to be the only author who gives structural details of this condition, which he describes as having been observed by him in a haddock, a carp, and a bleak. The basal axis of the skull is again always shortened. In the bleak this axis showed a single sharp ∧-shaped curve opposite the middle of the orbit. In the haddock there were two sharp curves, one opposite the orbit and the other in front of that. Lastly, in the carp the basal axis of the skull remained straight, but was extremely shortened in the region underlying the brain-box and behind the eyes.

The skeletal elements forming the posterior (hyomandibular-quadrate) limb of the suspensorial arch are markedly reduced in size. At the same time, the bones forming the anterior limb of the arch, as well as the other bones of the head in front of the orbital region, tend to be smaller than normal. The mouth usually looks upwards as well as forwards, so that the condition is not unlike what is commonly described as pug-headedness, *e.g.* in dogs. The lower jaw, however, does not project freely beyond the upper one.

Causation. The causation is probably of the same nature as that on which the pug-headed condition depends.

DEFECTS OF THE LOWER JAW.

Grave defects of the lower jaw are less common than pug-noses or round-heads. The two best examples I have come across are provided by the gurnard (*Trigla gurnardus*).

One is a jar specimen in the Glasgow Corporation Museum showing a good large head of this fish severed from the body and mounted whole. The mandibular arch is extremely small, lying entirely under cover of the upper jaw and hardly reaching forward to the middle of the roof of the mouth. The chief prominence below the mouth is formed by the mesial portion of the hyoid arch. The other is a similar specimen described in some detail by Johnstone (*118*). Regarding the osteology of the lower jaw, this author notes that the angulars are not recognisable as separate elements, while the articulars are short and placed almost vertically. Joining the distal ends of the two articulars is a hoop-shaped element, which was taken as representing the united and ossified Meckelian bars.

Profound defects of the lower jaw sometimes accompany cyclopia (pp. 42, 44), but here survival will be impossible. Donnadieu (*58*), however, gives an account of an adult carp, showing what may be described as semi-cyclopia, accompanied by malformations of both upper and lower jaws. The muzzle is shortened; the eyes approach the middle line; the skull ends abruptly above the eyes; olfactory openings are wanting; the whole face looks downwards and to the right; the shortened upper and lower jaws are in great part united together, and the mouth is reduced to a small, somewhat circular, opening 3 mm. in diameter, lying below the right eye. Lowne (*146* p. 55) also notes an example in the carp in which there is deficiency of the face in front of the eyes, the lower jaw being defective. (See also p. 62.)

Causation. It seems likely that defective conditions of the lower jaw may arise in the two different ways already described in connection with cyclopia, pug-head, etc.—(1) as autogenetic developmental aberrations (probably the two gurnard specimens and certain examples of higher animals, including mammals, showing similar malformations), or (2) as the result of interference with normal development through pressure or some other factor external to the embryo itself.

HUMP-BACK AND ASSOCIATED CONDITIONS.

(Hog-back; shortening of body or of tail; twisting of body or tail.)

This deformity has been noted time and again, even in large-sized fish, not only among the *Salmonidae*, but also in many other families.

Salmonidae (*adult*). Barrington *10*; Couch *45*; Day *54* II. 98, 102; Günther *86*; Hofer (*96a* p. 307); Lowne *146* p. 94; Malloch *147a*; Ritchie *207*; Stoddart *239*; Yarrell *275*.

Specimens have been sent to the author by Henry Lamond, Esq., and others, and probably every angler of experience has had examples to his catch. As regards early stages, nearly every one who has paid attention to fish hatcheries, notes the occurrence of embryos, the bodies of which show practically every form, degree, and locality of curvature (Bugnion *34*).

Other Fishes:

Of other adult fishes the perch provides a number of instances, *e.g.* Day (*54* I. 4), Lowne (*146* p. 94), Houghton (*99* p. 4), Howes (*102a*). Examples in *Mugil chelo, M. capito, Anguilla* and *Labrax lupus*, are put on record by Nimni (*168*). A very striking example in the cod is described by Storrow (*241*). It has long been known that in certain localities, *e.g.* the Firth of Forth, the cod sometimes shows a particular deformation of the body due to shortening and coalescence of vertebrae (Cobbold *41a*), Dyce (*61a*), Smith (*228a*), etc. This is the so-called Lord Fish of Yarrell, and seems to have been counted by some naturalists as a separate species (see Smith *loc. cit.* and also Day *54* 276-8). In the sole, two instances are recorded by Howes (*102a*), while Lowne (*146* p. 94) has also a note on an example from this species. The former calls attention to Hyrtl's important paper (*102b*) on Synostoses in the vertebral column of fishes, and notes that examples were also described by

Erdl and Stannius. The papers by Hofer (*96a*), Freund (*70*)[1] and Pellegrin (*188*) should also be consulted.

Not many data are available regarding twisting of the body in the early stages of fishes other than the *Salmonidae*, but attention may be called to notes by Holt (*97*) on this condition as occurring in embryos of *Zoarces*, and by Williamson (*269a*) in those of the herring. Both these authors refer to observations on the influence of cold in producing the condition in question.

Structure. Hump-back and allied deformations of body or tail may be accompanied by the following modifications of the vertebral column.

(*a*) Coalescence or synostosis of the vertebral centra in groups of several (*e.g.* 2 to 6) segments, while the neural and haemal spines, the muscle masses, and the spinal nerves retain their normal number. An excellent example is described by Ritchie (*207*), and another cited by Howes (*102a*) from Hyrtl (*102b*). The specimens described by Smith (*228a*), Cobbold (*41a*), and Dyce (*61a*), referred to above, also belong to this type. The condition is noted by Tornier (*249*) as being characteristic of some of the races of goldfish. It is usually, if not always, accompanied by increase in the transverse diameter of the affected centra, which may be so great that the weight of the fused centra exceeds that of an equal number of normal ones (Howes *102a*). There is also shortening in the antero-posterior direction, which may be so extreme that four or five coalesced centra occupy less than the length of two normal ones.

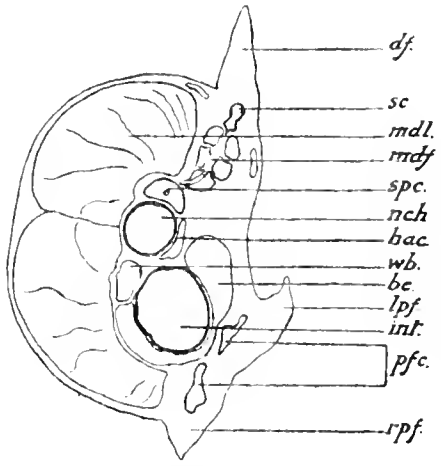

FIG. 6.—Transverse section through posterior part of body of an advanced *Salmo fario* embryo, showing curvature and deformation due to the condition described under (*f*). *bc*, body cavity; *df*, dorsal fin; *hac*, haemal arch cartilage; *int*, rectum; *lpf*, left pelvic fin; *mdl*, dorso lateral muscle mass; *mdf*, small muscles connected with the dorsal fin; *nch*, notochord; *pfc*, pelvic fin cartilage; *rpf*, right pelvic fin; *sc*, supporting cartilage of fin ray; *spc*, spinal cord; *wb*, Wolffian body.

(*b*) Simple shortening of the length of the vertebrae with increase in their transverse measurements, but without fusion of centra. This is said to occur in goldfish races (Tornier *249*). Mr. J. Ritchie, in a note to me, states that he has found a similar condition in certain fish from the Firth of Forth. Lowne (*146* p. 122) catalogues a specimen of the sole in which there is arrested development of 12 post-anal vertebrae, "the bodies of which have only about half their usual length and look as if they had been pressed together." Probably the condition in question grades into that described under (*a*).

(*c*) The backbone may show twisting or curvature without coalescence of vertebrae. Perhaps the most striking examples are those described by Howes (*102a*) in a sole, and by Storrow (*241*) in a codfish. In both there are five sharp sinuosities. The vertebral bodies are complete in number, independent, and only modified in shape so as to suit their position in the curves. Howes notes the interesting point that the neural and haemal spines are altered (by shortening, change of slope, etc.) so as to conform as far as possible to a normal body outline. The length of the body is, however, very distinctly lessened and its dorso-ventral diameter increased. A second sole described by Howes (*102a*) has its vertebral column curved only in the anterior region. Three distinct sinuosities occur in the backbone of a perch referred to in the same paper.

(*d*) In a specimen of the sea trout (*Salmo trutta*) sent to the author by Henry Lamond, Esq., a shallow notch in the contour of the dorsal surface of the fish behind the dorsal fin was marked internally by an entire absence of one of the neural arches, and a semi-fibrous condition of the dorsal portion of the succeeding myomere. None of the spinal nerves was missing.

[1] This anthor notices a number of other records, chiefly from papers to which I have not had access, and thereby adds to the above list examples from *Acanthias*, *Amia*, *Crenilabrus*, *Esox*, *Gymnotus*, *Leuciscus*, *Mormyrus*, *Mullus*, *Phoxinus*, *Polypterus*, *Tinca*, and *Trigla*. From Pellegrin (*188*) we have further to add *Cobitis* and *Scomber*. Hofer quotes the statement from Hnbrecht (*Klassen u. Ordn.* 6. Abt. 1-3, p. 60), that in shark-like fishes, pathological coalescence of vertebrae is commonest at the places of connection of the paired fins with the vertebral column.

(*e*) Some of the sharpest twistings are exhibited by hemididymous or mesodidymous forms, after exhaustion of the yolk store.

(*f*) Irregular curvature may be associated with absence, more or less complete, of the great lateral muscle masses on one side. In a crooked specimen examined by the method of serial sections, I found that a short distance in front of the vent the muscle masses vanish quickly and completely on the left side (Text-fig. 6).

The blank thus left is filled up in small part by loose connective tissue, but is chiefly compensated for by the mid-dorsal and mid-ventral structures curving round so as to encroach on the left side. In this manner the dorsal edge membrane and the left pelvic fin approach each other until they are separated by less than a fourth part of the circumference of the body. All the other organs tend to be displaced or modified in form so as to suit the new shape. A transverse section in front of the vent is illustrated in the accompanying figure. Just behind the vent the proper muscle tissue of the left side reappears, but in an exceedingly incomplete manner, and this condition persists to the end of the tail, which never fully recovers its bilateral symmetry. The tail fin is bunched together so that at first sight it appears to be absent. I would refer the origin of this deformity to an early katadidymous condition, in which, later, the left component became completely lost.

Causation. We are still in the dark as regards the general question of the causation of "twisted bodies" and the allied deformations. No doubt they are mainly congenital, and it is probable that their production depends on some very early developmental aberration capable of being induced by the action of external factors. But I believe the corollary is that (as in pug-head, cyclopia, etc.), certain forms of this defect are likely to appear from time to time spontaneously, by abrupt autogenetic variation. In the latter case they may be transmitted to descendants provided they permit growth and survival into adult life. Thus the goldfish races referred to by Tornier (*249*) indicate that in some of its forms the condition is hereditary, and the same thing is very strongly suggested by various facts relating to the widely distributed and constantly recurring *Lord-fish* type of cod, although Day and others class this type among "diseased" forms.

Mechanical injury has naturally been thought of as a possible cause. Thus Day (*54*) suggests that the hump-backed condition of many trout in certain hill streams might be due to violence through rolling over small cascades and falls at an early stage. Experimentally it is stated that twisted body is one of the defects that tend to appear if developing eggs are subjected to mechanical disturbance, or to unfavourable influences of other kinds. Holt (*97*) quotes Ryder as giving some data on the influence of cold on its production, while Williamson (*269a*) refers to similar data noted by Meyer for the herring.

In certain twisted trout embryos examined by the method of serial sections I noted the presence of premature calcifications within the sheath of the notochord. Conceivably, localised conditions of this kind might, by preventing normal axial elongation, lead in some cases to curvature of the backbone and in others to shortening without curvature. The membranous character of the ossification in the formation of vertebral centra seems highly favourable to coalescence of centrum-units wherever very marked antero-posterior shortening occurs, especially if the shortening be accompanied by tissue irritation such as pressure might produce. Something of the kind is perhaps indicated by the fact (Howes *102a*) that the weight of the shortened coalesced centra may be greater than that of an equal number of normal ones.

It has been suggested (Bugnion *34*, Howes *102a*) that the body muscles may be primarily at fault, through undue rigidity, contraction, or failure in growth. There is no convincing evidence for this view, however, except in the type described under (*f*) above, and here the original defect must date as far back as the period of actual formation of the muscle plates.

It need hardly be added that the condition is likely to be due sometimes to ordinary pathological conditions, for example, to inflammation, or to some other form of bone disease.

LOCAL DEFICIENCY OR REDUPLICATION OF THE NOTOCHORD.

In examining serial sections of trout embryos I have come across three cases of local *reduplication* of the notochord. In two of them the notochord is bifid at its anterior extremity, becoming single while still in the intra-cranial region. The parachordal cartilages are broad in front and enclose both ends of the notochord. There is no duplicity of any other structure. It is perhaps remarkable that one of these embryos was a cyclops of type B (pp. 41-42).

The third example of reduplication of the notochord was observed in sections which had been cut from an apparently normal embryo for the purpose of serving as a typical series. In the middle abdominal region the notochord divides into two limbs which lie adjacent to, but quite separate from, one another for four or five segments, and then unite again. Where they are widest apart each has a separate sheath and separate sets of neural and haemal arch cartilages. The adjacent cartilages are disposed exactly as in double monstrosities at the region of transition from the double to the single condition. These cases seem to be examples of local fission affecting a single axial organ, rather than examples of true axial duplicity.

Local *deficiency* of the notochord occurred in one specimen. Here the notochord, which is normal in the cranial and cervical regions, ceases abruptly just behind the level of the pectoral fins. After being absent for six somites, it reappears and runs backwards normally along the rest of the trunk. Plate XXVI. fig. 113 illustrates a transverse section in the defective region. The neural and haemal arch cartilages have fused together to form a series of half-rings below the cord. Ventral to these the lateral muscle masses meet one another in a mesial raphe above the dorsal aorta, forming a strong support and sling for the vertebral column and the cord.

ABNORMALITIES OF FINS.

(*a*) Excess. *Examples*:

Salmo irideus, a supernumerary pair of pectorals (Mazzarelli *154*);

Salmo fario, a supernumerary dorsal (Seligmann *226*);

Salmo fario, two dorsals side by side (observed by the author in a recently hatched embryo);

Siluris glanis, a small supernumerary pelvic almost median in position, but belonging to the right side (Warpachowski *267*);

Pleuronectes platessa, a well-formed four-rayed fin near the middle line just behind the two normal six-rayed pelvic fins (Duncker *59* 376-8);

Pleuronectes platessa, an abnormal precaudal fin frill on the left (*i.e.* under) side (Boulenger *30*) and M'Intosh (*155*);

Acanthias vulgaris, an almost median accessory fin on the top of the head (Grosser and Przibram *85*);

Raia clavata, an upright, oval-shaped dorsal fin in middle of back (Day *54* II. p. 344); a pair of rudimentary pectoral fins on the back (Gervais *80*);

Raia batis, two examples of accessory fins, both being of the paired-fin type (Rennie *203*).

In various goldfish races there occur: (1) excessive growth of a fin or portion of a fin, and (2) partial or complete doubling of certain fins, *e.g.* of the caudals and anals. The latter condition may be accompanied by doubling of the fin-ray supports and of the inferior spinous processes of the last two vertebrae (see Bateson *19* pp. 451-454). O. Storch (*240a*), who describes in detail the muscular and skeletal elements of the paired anal fins in the "Rinkin" variety of goldfish, argues that we have here the key to the evolution of the true paired fins. In this view these fins have not taken origin from lateral fin membranes, but have arisen by the splitting of portions of a median fin, while the limb-girdles have been evolved in response to the new dynamical conditions at the bases of these fins.

The lung-fishes supply a number of examples, among which may be noted:

Protopterus, a bifid right pectoral (Albrecht *1*); a trifid left pectoral (Boulenger *28*, Hopley *98*);

Lepidosiren, an instance in which the extremities of both pectorals underwent some degree of branching (Goeldi *82*).

Barfurth's Petromyzon larva with trifid tail should again be noted (see p. 36 of this work).

Causation. Certain cases of supernumerary fins are due to the persistence of an embryonic twin rudiment in this form. The instances recorded by Mazzarelli (*154*) and Gervais (*80*) appear to be of this kind, and possibly also those given by Rennie (*203*). It is by no means uncommon to find among broods of young trout towards the end of the embryonic stage examples of parasitic twins, in which one or both of the pectoral fins are the chief remaining structures. Lereboullet's (*143*) work on the pike provides an occasional example of this kind observed during actual development.

The doubled dorsal fin which I observed in a recently hatched trout embryo could best be accounted for as being due to a healed-up partial mesodidymus.

For other cases the somewhat theoretical explanation may be advanced (Rennie *203*), that there has been an attempt at independent development on the part of germ-cells that have somehow wandered or become separated from their proper locality. Or one may speak simply of hypertrophy with excess of the particular fin-forming embryonic material, and draw comparisons with examples of malformation by excess in other structures, *e.g.* digits (M'Intosh *155*).

Certain instances are clearly due to supra-regeneration after removal or to undue growth following injury or irritation. This applies particularly to the Dipnoan cases and, according to Boulenger (*30*), to that recorded by him in the plaice.

The goldfish races provide examples of great germinal variation, the extreme forms of which have been preserved and accentuated by selection.

(*b*) DEFECT. *Examples*:

(1) *Absence.* The following cases may be noted: *Cyprinus*, with tail fin awanting, Otto (*178* p. 133), Fiebiger (*68*), Nusbaum (*173*); *Esox lucius*, with false tail fin (Hofer *96*); *Abramis blicca*, without pelvic fins (Brindley *32* and probably same specimen Lowne *146* p. 112); *Acanthias vulgaris*, without second dorsal and caudal fins and with tail deformed (Grosser u. Przibram *85*); goldfish races with dorsals awanting (Tornier *249*); *Ameiurus natalis* without trace of pelvic fins (Eigenmann and Cox *62*). See also p. 61.

(2) *Defective development.* Goldfish races with various fins extremely reduced, Tornier (*249*); *Cyprinus* with reduced dorsal, Otto (*178* p. 266): *Raia clavata*, showing notch between the head and the anterior edge of the pectoral fins, so that the latter sticks out as a horn on either side of the former, Day (*54* II. Pl. CLXXI. 2), Traquair (*253*), Johnstone,[1] Vaillant (*262*), Williamson (*270* p. 54); cyclopic *Myliobatis*, with similar horns, Paolucci (*181*); misshapen spines and rays in the anal fin of *Sebastes*, Jaquet (*111*); deformed caudal fin in *Motella*, Jaquet (*112*).

Duncker (*59* 375-378) refers to a number of minor abnormalities in the fins of the genus *Pleuronectes*, *e.g.* reduction in size of the pelvic fins; blanks in the series of dorsal and anal fin rays; rays developed only in their proximal or distal parts; doubled rays; fusion of distal ends of fin rays; fusion of edge of right pectoral fin with the adjacent skin.

Numerous instances are on record of flatfish with the anterior extremity of the dorsal fin ending abruptly, so that a notch occurs between this fin and the head. The condition is usually associated with abnormal pigmentation of the under side, and often also with incomplete migration of the eye belonging to the side in question (see p. 56).

Causation. No single factor is sufficient to explain all cases of defective or absent fins. It seems necessary to assume the following as possible causes: (1) injury or removal followed by healing, and in some cases by partial regeneration; (2) arrest of development due to external causes acting during embryonic life, or in the early stages of growth; (3) spontaneous germinal variation, or reversion. Probably the first four cases cited under *Absence* belong to the category of injuries, while the *Acanthias* provides an example of induced arrest, and the remainder are mainly due to the third of the causes named above, though some of them may be referable to the others.

[1] Report, 1905, Lancashire Sea Fisheries Committee, p. 188.

(*c*) The so-called "Tailless" Trout.

Reference is made to this condition by Couch (*45*), Day (*54* II. p. 102), Stoddart[1] (*239*), Peach (*185*), and Traquair (*251-2*). The latter gives a full account of the general appearance and the structure of the fins affected, as well as a discussion of the probable causes, and his papers may with advantage be consulted for fuller details. In these trout, neither tail nor tail-fin is awanting, but the rays of the latter are abnormally shortened and thickened at their extremities, which tend to be bent upwards or downwards towards a median posterior angular projection. In the specimens described by Traquair from Islay and Kirkcudbrightshire, the extremities of the rays, besides showing a tendency to coalesce, were deficient as regards dichotomisation and also as regards the number of their transverse joints. Specimens from the River Carron showed the same general features, except that the amount of dichotomisation at the ends of the fin rays was not reduced.

It is important to note that the caudals are not the only fins affected. The anals usually share in the malformation, the pectorals often, and more rarely the pelvics. The dorsal fins seem never to suffer.

The causation is unknown. Traquair (*254*) gives an excellent analysis of the available evidence on the subject.

ABNORMALITIES OF COLORATION.

(*a*) *In Fishes generally.*

Ordinary variations and abnormalities of coloration hardly fall within the scope of this work. The larger systematic books on fishes contain mention of such variations in numerous species, and reference may be made to the literature index (pp. xi-xvii) for the following papers or notices dealing with the subject: Bateson (*19* p. 466); Bellotti (*21*); Berg (*22*); Bird (*24*); Bolau (*26*); Dean (*55, albinism*); Günther (*87*); Kershaw (*122*); Ninni (*170*); Panceri (*179, albinism*); Pettis (*191, albinism*); Schneider (*220*); Suomalainen (*243*); Tornier (*249*); Traquair (*255*); Trois (*257-60*). Attention should also be called to the important work of Cunningham and MacMunn (*50a*) on the coloration of the skins of fishes, and to that of Schondorff (*221*) and Wagner (*Intern. Rev. Hydrobiol.* Leipzig 4 1911 pp. 1-33) on the normal pigmentation of the *Salmonidae*.

(*b*) *In Flat Fishes.*

This group requires separate mention. To begin with, its members are subject to the same minor colour variations as occur in other fishes, for example to *albinism*, usually partial in character and patchy or local in distribution.

Of much greater importance is the so-called ambicoloured condition, in which the whole or part of the under side is more or less deeply pigmented. If not very pronounced or complete, the condition may be unassociated with any other abnormality. Instances of the kind have been recorded in *Pleuronectes flesus*, *Pl. oblongus*, *Pl. microcephalus*, *Pl. platessa*, *Pl. limanda*, *Solea vulgaris*, *Rhombus maximus*, and *R. laevis*, while *Pl. cynoglossus* normally has many chromatophores (50 per sq. cm. (Elmhirst *64*)) on the under side. Bateson calls attention to the fact that in the better marked examples of this and the succeeding sets of cases there is often correspondence in character and position between the abnormal colour markings on the under side and the normal ones on the upper side. This correspondence seems to depend primarily on the persistence and further development of chromatophore groupings normally present in the larva. It does not accordingly furnish a pure illustration of *Homoeosis, i.e.* the acquirement of secondary or "imitative" bilateral symmetry (see Bateson, *17*, *18*), although this principle must be in operation in regard to minor and specific details.

Pronounced and widespread pigmentation of the under side, particularly when the head is wholly or partly involved, is found to be associated:

[1] See footnote on p. 46.

(*a*) with shortening of the cranial attachment of the dorsal fin, so that the tip of this fin reaches forward for some distance as a free hook-shaped process;

(*b*) with the presence of spines, tubercles, or rough scales on the under side simulating in some degree those which are normally found on the upper side. In addition, there may be unusual thickness of the muscular layers, and undue pigmentation of the peritoneal lining, on the under side;

(*c*) often also with abnormality in the position of the eye belonging to the under side, which looks as if it had not completed its migration. In well-marked instances the eye in question may not have travelled further round than the (apparent) dorsal edge of the head and may accordingly be partly visible from the blind side of the fish, as in the so-called "cyclopean" condition. Or more commonly, both eyes may be on upper side of the head, but lying a little wider apart than normal and approximately in the same transverse line.

References to the earlier literature on the subject of these abnormalities are given by Bateson (*19*, 466-473), and Cunningham and MacMunn (*50a*). The former quotes Steenstrup as stating that hooking of the dorsal fin has been observed in all flat-fish, except the halibut (*Hippoglossus*). For the turbot (*Rhombus maximus*) Cunningham makes the generalisation that hooking of the dorsal fin is present in all ambicoloured specimens which show pigmentation on the under side as far forward as the preopercular region, the tip of the dorsal fin, and the lower jaw. In this species the rest of the under side of the head seems hardly ever to be pigmented. In ambicoloured flounders, however, the whole of the under side may show pronounced pigmentation.

Of instances later than those which are noticed by Bateson (*loc. cit.*), we may quote the following:

(1) Cases in which the ambicoloured condition is associated both with hooking of the dorsal fin and with abnormality in the position of the eye:

Pleuronectes flesus,	Cunningham (*50 a*), Elmhirst (*64*), M'Intosh (*155*, two specimens);
Pleuronectes platessa,	Cunningham (*50 a*, noted by Dr. Brandt, Kiel);
Pleuronectes italicus,[1]	Ninni (*169*);
Pleuronectes limanda,	Elmhirst (*64*); Vaillant (*201*);
Rhombus maximus,	Cunningham (*50 a*), Ritchie (*206*, eyes *approximately* normal in position); Elmhirst (*64*), Sacchi (*211*), M'Intosh (*155*, four specimens);
Rhombus laevis,	Filhol (*69*), Johnstone (*119*);
Solea vulgaris,	Ninni (*169*), Cuénot (*46*).

(2) Cases in which the ambicoloured condition is associated with a fin abnormality, but apparently not with any marked abnormality in the position of the eye: *Rhombus maximus*, *Rh. laevis*, *Pleuronectes flesus*, *Pl. platessa* Cunningham (*50a*, *50*), *Pl. platessa*, Elmhirst (*64*).

The *Rh. laevis* mentioned under (2) above as having been described by Cunningham is of particular interest. In the first place it is a reversed specimen, and in the second place the upper surface of the body is extremely deficient in pigment, except anteriorly, where a certain amount occurs in the head region, especially between the eyes and around the dorsal eye. The lower side, on the other hand, is deeply, but not uniformly, coloured, pigmentation being absent from the head and from the dorsal region above the head. The specimen was very young (4·4 cm. in length).

In this connection it may be noted that one of the ambicoloured plaice recorded by Elmhirst (*64*) was almost white on the upper side in the posterior quarter of the body, and had the dorsal fin not reaching to the head but ending over the origin of the pectorals.

Mode of Origin and Causation. It seems to be certain that in most flat-fishes (*Plagusia* being

[1] A careful analysis of the differences between this specimen and a normal *Pl. italicus* is given by Ninni (*169*), from which the following points may be noted, in addition to the three principal ones which have been named: The form of the body is elongated instead of being oval; the mouth opening is almost vertical instead of being oblique; there are well-marked tubercles on the under side; the interorbital space measures 4 mm. instead of 1 mm. The lateral line makes a very slight bend above the pectorals instead of a somewhat pronounced curve. The contour of the preopercular is well marked instead of being hardly distinguishable. The pelvic fins are equal, and the pectoral fin on the upper side is as large as that on the blind side, instead of being somewhat smaller.

an exception) the migration of the eye from the blind side takes place prior to the forward extension of the dorsal fin. Speaking in mechanical terms, one may say that marked *incompleteness* of migration is able to interpose a direct obstacle in the way of this extension, *e.g.* in the "cyclopean" types. On the other hand, simple *delay* in the migration may hold back the extension in question till the fin- and cranial-tissues have lost their early powers of mutual union and growth. The delayed migration of the eye may in the end be fully carried out, *e.g.* in the instances mentioned under (2) above, or it may remain somewhat incomplete, as in the numerous instances where the eyes are set slightly further apart than in the normal condition.

Probably, however, the arrested migration of the eye is significant, less from actually obstructing the forward growth of the dorsal fin, than in being an expression of a general aberration of development involving other departures from the normal moulding of the head, some of which fall under the category of *excess*, and others under that of *defect*. As Traquair (*251a*) pointed out, the dorsal fin of a flat-fish does not extend forward in the morphological middle line of the head, but is distinctly to the blind side of this line. One of the defects may well be that a new mid dorsal *edge* of the head is never prepared at all or never twisted round sufficiently to enable it to unite with the dorsal fin.

Among characters indicating excess, we may place the undue development of spines, tubercles, etc., on the under side. This can occur without pigmentation of the side in question. As Bateson points out, it must be put down in the main not to reversion or atavism, but to the principle of *Homoeosis, i.e.* to the tendency towards secondary or "imitative" bilateral symmetry.

An interesting attempt at analysis of the germinal factors involved has been made by Cunningham in connection with his description of the brill (*R. laevis*), to which attention was previously drawn. He suggests that the determinant system of the ovum may have been altered in such a way as to match a *reversed* flatfish type of body, with a *normal* flatfish type of head, the resulting misfit being evidenced by the condition of the dorsal fin.

This might account for the presence of pigment on the under side of the body and its absence from the under side of the head. The upper side of the body, though white at first, would darken later, since, as Cunningham had previously shown (*50a*), pigmentation can be induced *even on the under side* of a flat-fish, through exposure to light. The theory fails when applied to ambicoloration in the flounder, since specimens not infrequently occur in which the under side of the head is pigmented as well as the under side of the body. Again, as Cunningham himself points out, it does not explain the presence of the characteristic spines and tubercles which occur on the upper side of ambicoloured as of normal flat-fish. The arrested migration of the eye is also not satisfactorily accounted for, and on the whole the explanation besides depending on theoretical conditions does not carry us as far as the facts themselves.

As Cunningham rightly emphasised, the point which needs explanation is that in ambicoloured flat-fish the under side of the head is usually either unpigmented or has less pigment than the rest of the under side. One might suggest the following consideration as supplying a not too far-fetched reason. Whiteness of the under side is not merely a reduction phenomenon, but is of importance to fishes in general by rendering them less conspicuous in the water, and thus enabling them more readily to obtain food or escape from enemies. This does not apply in the ordinary way to flat-fish, but even to these it is likely to be of some importance in feeding,[1] that the head as seen from below should not appear so conspicuously black as the presence of pigment, together with the want of incident light, would make it. Whiteness of the under side of the head (and in a less degree of the parts adjacent) might thus come to be a character of positive importance, and accordingly less liable to variation, than the condition as regards colour of the rest of the under surface, a condition which is traceable more directly to simple reduction. Even in Cunningham's own experiments, it was only slowly and with difficulty that pigment could be induced to appear on the blind side of the head.

That in most cases the origin of the complex of abnormalities under discussion is a germinal

[1] *Crustacea* and *Polychaeta* seem to be staple articles of diet with certain flat-fish, *e.g.* the plaice (Masterman in Vol. XIII. *Des Rapports et Procès-Verbaux du Conseil International pour l'Exploration de la Mer*, Jan. 1911, p. 17).

one there can be little doubt. I believe, on general grounds, that it will also be found capable of being produced by the action of external factors, but meantime direct experimental evidence on the question is awanting. M'Intosh (*155*) has noted two points of great interest, (*a*) that in Pleuronectids which are metamorphosing normally, the future under side is paler than the other, even before the young fishes begin to swim obliquely or to leave their pelagic habit of life; (*b*) that in particular instances where the pelagic life was unduly prolonged, the same lessening of colour occurred.

REDUCTION AND PARASITISM.

This condition occurs in each of the classes of double monsters. All degrees of reduction on the part of the minor twin may have been attained even before the end of embryonic life. In the adult, supernumerary paired fins (p. 54) are probably the structures which most readily give evidence of an originally double condition, obscured later by almost complete degeneration of one of the components. Lereboullet's work provides cases in which the process of reduction of a twin rudiment was actually observed in the embryo. In the trout, out of many examples, I shall only select two for particular description, and both of them belong to Class I. (p. 12).

The first specimen is in some respects unique. My attention was directed to it by the presence of an interruption or cleft in the right upper jaw, producing the appearance of a right-sided harelip in what seemed to be, in other respects, a normal newly-hatched trout embryo. On cutting serial sections, I found that a small additional eye lies at the bottom of this cleft, in the roof of the mouth, to the right side of the middle line, and in the same transverse plane as the normal eyes. This eye is embedded in confused muscular tissue, has a well-developed lens, a small retina, no choroidal fissure and no choroidal gland. Its optic nerve is represented by a small bundle of fibres which sweep over the edge of the retina to join the right normal optic nerve (Pl. XXIV. fig. 105). The retina is small and elongated antero-posteriorly. The pigment-layer is present as such only in the posterior half of the retina. Anteriorly, the corresponding layer is non-pigmented, richly cellular, and becomes continuous with the brain-wall just in front of the optic recess, in such a way that the central cavity of the brain is prolonged into the space between the retina and the pigment-layer. An optic stalk, embryonic in condition, is thus present.

Two deep grooves are found in the floor of the third ventricle and the mid-brain, each leading down into a separate infundibulum and hypophysis. The grooves are separated by a considerable ridge of brain-tissue. The right hypophysis and its hypoaria are somewhat compressed; the rest of the brain is normal. The right palato-quadrate bar is absent and the trabeculae cranii are displaced to the left.

Taken by itself, the supernumerary eye might seem to be simply a case of repetition, since its nerve is derived from the right optic nerve. But the persistence of an embryonic optic stalk, together with the presence of a double hypophysis in the brain, would seem to indicate that the explanation is to be found in an extremely local degree of axial duplicity. It is not clear, however, whether the accessory parts are to be looked upon as being the remains of inner (adjacent) structures in a double-head, or as representing a reduced second head. A somewhat analogous case is described by Gurlt (*Lehrbuch der pathologischen Anatomie*, ii. Theil, p. 221, Berlin 1832). In this instance the right ramus of the lower jaw in a lamb has an accessory ramus on its inner side with an accessory set of molar teeth. The tongue is double anteriorly. There are two pituitary glands and two infundibula arising from a single large tuber cinereum, two pineal glands, three pairs of corpora quadrigemina, and two aqueducts of Sylvius. Three accessory nerves, arising from the mid-ventral line of the brain, go to an "ocular rudiment in the sphenoid." This account is quoted from Taruffi (*Storia della Teratologia*, vol. iii. p. 115). For other examples of duplicity of the hypophysis see Ahlfeld (*Die Missbildungen der Menschen*, p. 73, Leipzig 1880) and Bland Sutton (*Transactions of the Odontological Society* (*Dental Record*), 1888, pp. 73-78).

In the trout, if new and more definite cases of the kind described above become available to found on, it may be necessary to institute a Class of anadidymi which will come in front of

my Class I. (p. 3) as showing duplicity in a still less marked degree. Meantime we do not need to do more than call attention to this possibility, pointing out in its favour that Barbieri's (*7*) early double trout embryo exhibited much greater doubling in the floor than in the roof of the brain, while Lereboullet (see p. 11) showed in general that a very considerable degree of early axial duplicity can afterwards become completely or almost completely lost, through the working of secondary fusion. Schmitt's Group 7 makes provision for some such Class. At the same time, the little that is known on the subject, renders the alternative possible, that obscure and limited cases of axial duplicity may have had their origin in union of the *longitudinal* or *parallel* type (p. 29).

The second specimen I shall describe under the heading of Reduction was quite normal in appearance, except for the presence of a tiny refractive knob behind the left eye. Examination of serial sections shows the knob to contain a lens of considerable size, enveloped in muscle-fibre, but unaccompanied by any other eye-structure, and lying in front of an exceedingly minute fore-brain and third ventricle. The cavity of this third ventricle communicates with the mid-brain cavity of the normal head (Pl. XXIV. fig. 106). The embryo was quite lively when obtained, and its chances of survival would probably not have been appreciably diminished by the small tumour in question. It will be seen from fig. 2 that the functional eyes and fore-brain belong to a predominant *right* twin head, as also do the olfactory organs, the mouth, and the anterior cranial cartilages generally. The back part of the brain and the whole of the body are, however, composite, since their left moiety represents structures which are continuous with the left side of the left (aborted) twin, while their right side is a continuation backwards of the right side of the right twin. This gives an even more complex mixture of "individualities" than is found in ordinary cases of symmetrical double monstrosity.

PATHOLOGICAL CONDITIONS OF THE OVUM OR EARLY EMBRYO.

Some of these have been referred to already, for example under the last two of Lereboullet's types (p. 10). Numerous single instances may be found throughout this author's account of his observations. Attention should also be drawn to Rauber's description of the following anomalous conditions in the development of pike and salmonid eggs (*202* **5** (668-702)).

(*a*) Examples (salmonid) just at the end of segmentation, of blastoderms showing irregularities of outline or surface, and want of uniformity in the size of the segmentation cells.

(*b*) Instances (salmonid) in which the margin of the blastoderm has failed completely, or almost completely, to become thickened in order to give rise to the embryo-rudiment. In such cases the blastoderm may extend as far down as the equator or even the lower pole of the egg. The growing margin tends to become irregular, showing projecting angles and lobes.

(*c*) Defective formation of the anterior, middle, or posterior portions of the embryo. Five examples of salmonid eggs are given in which the anterior part of the embryo is defective; three of the pike in which the anterior and middle portions are wanting; one (salmonid) in which the middle and posterior portions are defective, and another salmonid in which the embryonic rudiment has not been formed at all.

(*d*) Partial or total dehiscence of the body halves. This condition is referred to under Mesodidymus (p. 25).

(*e*) Oblique position of the embryonic rudiment. Several examples were noted in the salmon.

Girdwoyn (*81*) makes reference to embryos without eyes, with both eyes present but rudimentary, with only one eye and that in its normal place, with well developed head but rest of body rudimentary, without head but with developed body, etc. Loeb (*145*) describes fish embryos without circulation, while Stockard (*236*) and others refer to various pathological conditions produced in the course of their experiments.

ADDITIONAL ABNORMALITIES.

Having reference for the most part to single organs.

Barbels. Additional barbels in *Ameiurus natalis* (Eigenmann and Cox *62*). Doubling of a regenerated barbel in *Silurus* (Roth *209*).

Brain. Anomalous cerebellum of *Alopias* (Leger *138*).

Torpedo embryo with a neuro-epithelial organ in relation with the cerebral ganglia (Coggi *40*).

Eyes.

Absence of one eye. Giraldus Cambrensis (III. c. x.) speaks of eels, trout and perch existing in the lakes of Snowdon which only possessed the right eye but were invariably blind with the left (quoted from Day *54* II. p. 102). It is stated somewhere that fish with only one eye are still from time to time caught in the district named.

Lowne (*146* 525-6, pp. 124-5) catalogues the head of a large carp with entire deficieney of the eye on the left side, and the head of a barbel with absence of the right eye.

Williamson (*270* p. 53) describes an angler-fish with only one eye.

See also Stoddart (*239*) quoted in footnote on p. 46 of this work.

Atrophy. Mencl (*157*) records the presence of two lenses without other eye structures. Compare the case of parasitism described on page 60. A somewhat similar condition in which the lens alone of all the eye structures has survived is shown in Pl. XXVI, fig. 112, of this work, which illustrates a transverse section of a single atrophic head. The mouth, the lower jaw, the trabeculae, and the palato-quadrates are absent. One large lens, clothed with muscle-fibres, is present on the right side ventrally and compresses the lower part of the brain. A second smaller hour-glass-shaped lens lies beside it, all other ocular structures being deficient.

Egg, double. Vayssiere (*264*) describes an egg capsule of the porbeagle shark, which contained two separate ova, each with a growing blastoderm. A somewhat similar instance in *Scyllium* is recorded by Joseph (*120*).

Fins, absent or defective. The following instances, collated by Freund (*70*), fall to be added to the list on p. 55: a *Phoxinus laevis* with defective pelvic bones (Fatio), and another with an absent pectoral (Lunel); *Silurus glanis* with atrophic pectoral fin (Jaquet); *Leuciscus dobula* without pelvic fins (Martens); *Squalius cavedanus* without pelvic fins and with reduced pelvic girdle, carps without pelvic fins but with pelvic girdle and musculature (Hofer); goldfish without dorsal fins (Hofer); goldfish without left pelvic fin (Day); thirteen examples of *Gasterosteus pungitius* without pelvic fins or girdles (Day); goldfish with various other abnormalities of fins, including triple or even quadruple lobing of the caudal fin (Pavesi, Watase, Cori, Kishinouye). See Freund, *loc. cit.* p. 726-7. For other papers on goldfish, or references to goldfish literature, see Bateson (*19* pp. 309, 451, *453*), Pouchet (*194*), Ryder (*210*), Stoll (*240*), Storch (*240a*), Tornier (*249*).

Fin rays. Unusual elongation of second anal fin ray in *Proteracanthus* (Pellegrin *186*). Various minor abnormalities in *Cyprinidae* (Knauthe *125*). See also p. 55.

Gill absent in trout (Stoddart *239*) quoted in footnote on p. 46.

Gill-cleft. Reduction of the last gill-cleft in *Squalus acanthias* L. (Ekman *63b*).

Gill-tufts present instead of teeth (see under *Teeth*).

Gill-covers. Day (*54* II. 102) mentions trout from Maltham Tarn, Yorkshire, with imperfectly developed gill-covers, and Lowne (*146* p. 55) catalogues a similar specimen from Loch Assynt, Sutherlandshire. See also Miall (*158a*). Some further instances are given by Hofer (*96a*).

Gonads. Williamson (*270* p. 64) describes a partly hardened tough tuberculated ovary in the haddock, and Hefford (*91*) notes arrest of development in one gonad of a male conger.

Hernia. Mudge (*166*) describes an adult female dogfish with hernia of part of the stomach and certain other organs into the lumen of the pharynx.

Kidney. Howes (*100*) gives an account of variations in the kidney of *Raia clavata* which point in his opinion to a process of adaptative evolutionary change.

Lateral line. Supplementary in *Acipenser* (Jaquet *110*).

Do. Interrupted in a haddock (Mr. J. Ritchie, in a note to the author).

Mouth. Several instances have been put on record of fair-sized fish in which the mouth opening was either absent or minute, the condition being associated with other cranio-facial defects. Cases of the kind are noted by Laurence (*136a*) in *Sclerognathus*, and by Hofer (*96a*), St. Hilaire (*213* I. p. 285), and Steindachner (*234a*) in *Cyprinus*. Freund (*70* p. 719) also cites records from *Cyprinus* by Schiemenz and Bruyant.

The bones of the upper and lower jaw exhibit various degrees of defect or malformation, the actual closure or narrowing of the mouth being effected by skin or membrane extending over their representatives. Food must have entered the pharynx through the gill slits with the respiratory current.

It will be remembered that the specimen described by Donnadieu (see p. 51 of this work) had an extremely small mouth opening, and that a similar condition (p. 42) was found in one of my cyclopic trout embryos.

No doubt in its best marked forms the condition is a congenital one, although healing after wounds certainly accounts for many minor cranio-facial defects. A number of instances of this kind have been brought together by Hofer (*96a*) and Freund (*70*), while Garstang (*75*) notes a remarkable malformation in the mouth of the sea-bream, which he thinks was probably the result of injury.

Muscle. An abnormal superior oblique in *Carcharias* (Allis *3*).

Nerves. Variations in the pelvic plexus of *Acanthias* (Punnet *196*).

Notched body. Johnstone (*116*) describes a plaice with a large notch on the ventral edge of the posterior part of the body, and thinks that injury was the probable cause.

Ovaries. Three in a sturgeon (Grimm *83*). See also under *Gonads*.

Oviduct. Present in an adult male skate (Matthews *151*). See also Borcea (*27*).

Pyloric caeca. Branching in *Centrolophus* (Riggio *204*).

Respiratory organs. Variations in the lamprey and hag (Howes *102*).

Reversal (*Metastrophy*, Cunningham, *50*) seems to occur with varying frequency in all, or practically all, the species of flatfish. In this condition the side which is normally the *under* or *blind* side lies uppermost, and there is a corresponding interchange between the two sides as regards their external features and their ocular and cranio-facial characteristics. The viscera, however, retain their usual disposition. Thus alike in normal and in reversed flatfish the liver hangs down to the left side of the abdominal cavity and the coils of intestine are directed to the right (Cunningham, *50a* p. 861).

Scales. Increased number on one side in the pilchard (Bateson 15-16 and Lowne 146 p. 119).

Snout. Bifid tip of snout in *Acipenser ruthenus* (Jaquet, quoted in Freund *70* p. 719).

Spiral valve of Raia. Exhibiting a large degree of variation (Parker *183a*).

Teeth. Male *Raia* with blunted teeth (Day *54* II. p. 344).

Acanthias with gills instead of teeth in the upper jaw (Grosser *85*).

Rhinoptera, with abnormal dentition (Woodward *273*).

Telescope eyes of goldfish (Tornier *249*, and others, see above under *fins*).

INDEX TO STRUCTURES AND SUBJECTS.

The italic numbers refer to pages in the text, while the erect Roman and ordinary numerals refer to Plates and Figures. Cl. I., Cl. II., *etc. indicate different Classes of double monstrosity, while* s., trans., norm., horiz., *etc. are abbreviations respectively for section, transverse, normal, horizontal, etc.*

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Pls. XVII.–XXI. figs. 56–93, Pl. XXII. figs. 94–96, Pl. XXIV. figs. 100–106, are from drawings made by the author, and are based on the study of numerous series of sections. All the other plates and figures are from photomicrographs of specimens or sections.

Pls. I.–II. figs. 1–12.
Surface views of normal trout embryo, and of specimens belonging to various Classes of double monstrosity.

Pls. III.–IV. figs. 13–20; also Pl. VI. figs. 24–26.
Transverse sections of a normal trout embryo at the same stage in development as the monstrosities described. Compare with the sections, etc., of the latter, shown in the succeeding Plates.

Pl. V. figs. 21–23.
Horizontal sections of normal trout embryo, as above.

Pl. VI. figs. 27–29; also Pl. VII. figs. 30–31.
Transverse sections of double monsters with union in the posterior part of the body (Class VI. (*a*) and (*b*)).

Pl. VII. figs. 32–34.
Transverse sections through the triple monster described on pp. 33–34; see also Pls. XXII.–XXIII. figs. 94–99.

Pls. VIII.–IX. figs. 35–38.
Transverse section through the head of a double monster with union of the twin brains in the region of the optic lobes (Class I.).

Pls. X.–XI. figs. 39–42.
Horizontal section through the head of a double monster with union of the twin brains in the region of the optic lobes (Class I.).

Pl. XII. figs. 43–46.
Horizontal sections, as above, but in a specimen showing a different disposition of various parts.

Pls. XIII.–XIV. figs. 47–51.
Transverse sections through the head of a double monster with union of the twin brains in the region of the medulla (Class II.).

Pls. XV.–XVI. figs. 52–55.
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Pl. XVII. figs. 56–63.
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Pl. XVIII. figs. 64–72.
Figs. 64 and 65 illustrate the visceral arch cartilages, and Figs. 67 and 68 the vascular system in double monsters belonging to Classes I. and II. Fig. 66 shows the inner girdle and fin cartilages in an example from Class IV. (union in pectoral region, inner pectoral fins being present but united). Figs. 69–72 are diagrams to illustrate the cavities of the brain in a normal embryo and in double monsters belonging to Classes I. and II.

Pl. XIX. figs. 73–81.
Figs. 73–75 illustrate the heart in a normal embryo and in double monsters belonging to Class III. (union in pectoral region, adjacent pectoral fins not being represented) and Class IV. (union in pectoral region, adjacent pectoral fins being present but united). Figs. 76–81 illustrate the posterior ends of the Wolffian ducts, the bladders and urinary pores in a normal embryo and in double monsters belonging to Classes V. and VI. (union by the body or tail).

Pl. XX. figs. 82–87.
Fig. 82 shows the inner composite otocyst in a double monster belonging to Class II. (union of the twin brains at the medulla). Figs. 83–87 illustrate the glomerulus and the head-kidney and the first portions of the Wolffian ducts in normal embryos and in specimens belonging to Classes I. II. III. and IV. of double monstrosity.

Pl. XXI. figs. 88–93.
Diagrams with transverse lines to indicate the planes and levels of certain typical sections of which photomicrographs are shown in the earlier plates. The structures particularly illustrated are the brain cavities and the cranial and hyomandibular skeleton.

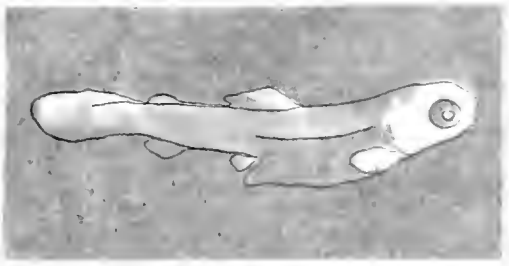
Pl. XXII. figs. 94–96.
These figures illustrate the external appearance and the alimentary and urinary structures of the triple monster described on pp. 33, 34.

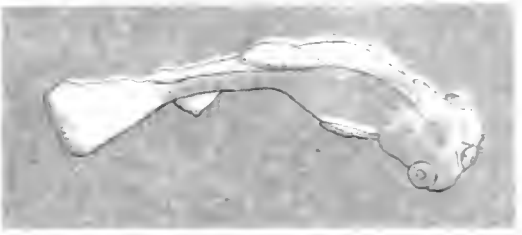
Pl. XXIII. figs. 97–99.
Transverse sections of the body of the triple monster; see also Pl. VII. figs. 32–34.

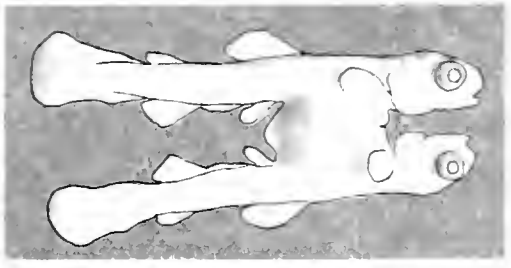
Pl. XXIV. figs. 100–106.
The figures illustrate cyclopia (pp. 40–45) and supernumerary eyes (pp. 59, 60).

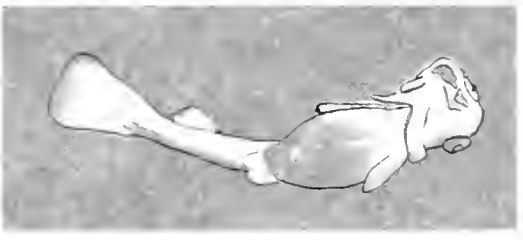
Pl. XXV. figs. 107–110.
Transverse sections through the ocular region in cyclopia and semicyclopia (p. 44).

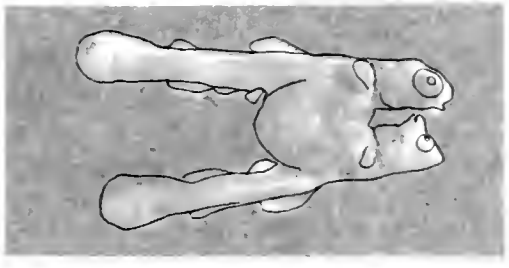
Pl. XXVI. figs. 111–114.
Fig. 111 follows Fig. 110 in illustrating semicyclopia; Fig. 112 shows the atrophic head referred to on p. 61; Fig. 113 is a section showing absence of notochord; and Fig. 114 a section behind the pectoral fins in a double monster belonging to Class IV.

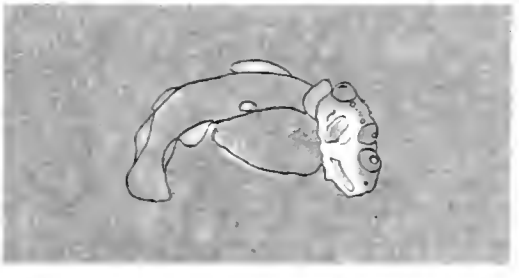












MARY OF CO

Pl. XXII [illegible]
[illegible] study of [illegible]
[illegible] specimens [illegible] section

[illegible] drawings made
[illegible] plates and figures

[illegible] embryo, and [illegible] specimens
[illegible] of double monstrosity.

[illegible] Pl. VI, figs. 24–26.
[illegible] [illegible] front embryo at the same
[illegible] [illegible] the monstrosities described
[illegible] [illegible] sections, [illegible] the latter, shewn in
[illegible] Pl. [illegible]

[illegible] [illegible] cle from Class IV.,
[illegible] [illegible] being present
[illegible] [illegible] illustrate the
[illegible] [illegible] more double

Horizontal sections [illegible] rooms [illegible] front embryo, as above.

[illegible] [illegible] figs. 27–29; also Pl. VI [illegible] figs. 30–31.
Transverse sections [illegible] double monsters with union in the
posterior part of the body (Class VI. (*a*) and (*b*)).

Pl. VII. figs. 32–34.
Transverse sections through the triple monster described
on pp. 33–34; see also Pls. XXII., XXIII. figs. 94–99.

[illegible] Pl. [illegible] figs. 35–[illegible]
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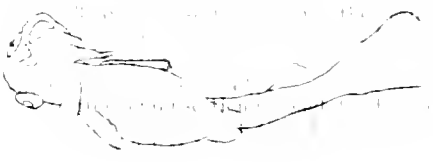

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FIG. 1. Side view of a normal trout embryo of same age as the monsters described. Sections of similar normal specimens are shown in Pl. III. figs. 13-16, IV. figs. 17-20, VI figs. 24-26 (transverse); and in Pl. V. figs. 21-23 (horizontal). Diagrams of skeleton, etc., in Pl. XVII. figs. 56, 57, 62, XVIII. fig. 69, XIX. figs. 73, 76, XX. fig. 83. Description on pp. 11-12. Contrast with Figs. 2-12. (× 3.)

FIG. 2.—Side view of a double trout embryo, with union by the yolk-sac only. See pp. 23-24. (× 3.)

FIG. 3.—Side view of a specimen similar to the last, but with one of the heads showing a condition of semi-cyclopia. See pp. 7, 44. Figs. 109-111, in Pls. XXV.-XXVI., are from sections of this specimen. (× 3.)

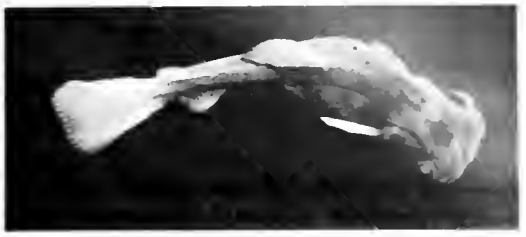


FIG. 4. View from above of a double monster belonging to Class I., *i.e.* with union of the twin brains in the region of the optic lobes. Transverse sections of a similar specimen are shown in Pls. VIII.-IX., figs. 35-38, horizontal sections in Pls. X.-XII. figs. 39-46, and diagrams of cranial skeleton, etc., in Pl. XVII. figs. 58, 59; XVIII. figs. 64, 67, 70, 72. Description under Class I. on pp. 12-15. (× 3.)

FIG. 5.—View from ventral aspect of the double monster illustrated in Fig. 4. Two mouth-openings are seen, separated by a septum containing the remains of the adjacent Meckelian bars. For references, see under Fig. 4. (× 3.)

FIG. 6.—View from below of a double monster belonging to Class II., *i.e.* with union of the twin brains in the region of the medulla oblongata. The two adjacent eyes are seen; also the two mouth-openings, separated by a thick septum containing the adjacent hyomandibular and Meckelian cartilages. Sections are shown in Pl. XIII. figs. 47, 48, and XIV. figs. 49-51. Diagrams of cranial skeleton, etc., in Pl. XVII. figs. 60, 61, XVIII. figs. 65, 68, 71. Description under Class II. on pp. 15-18. (× 3.)

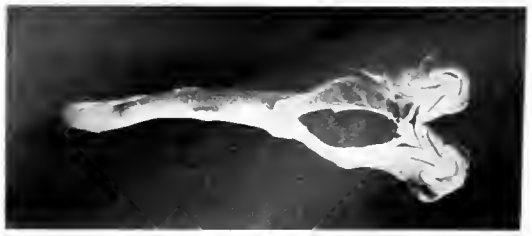


FIG. 7.—View from ventral aspect of double monster belonging to Class III., *i.e.* with union in pectoral region, the adjacent pectoral fins not being represented. Horizontal sections in Pl. XV. figs. 52, 53, XVI. figs. 54, 55. Diagrams of vertebral column, heart, etc., in Pl. XVII. fig. 63, XIX. fig. 75, XX. fig. 84. Description under Class III. on pp. 18-19. The body wall over the yolk is ruptured along the middle line. (× 3.)

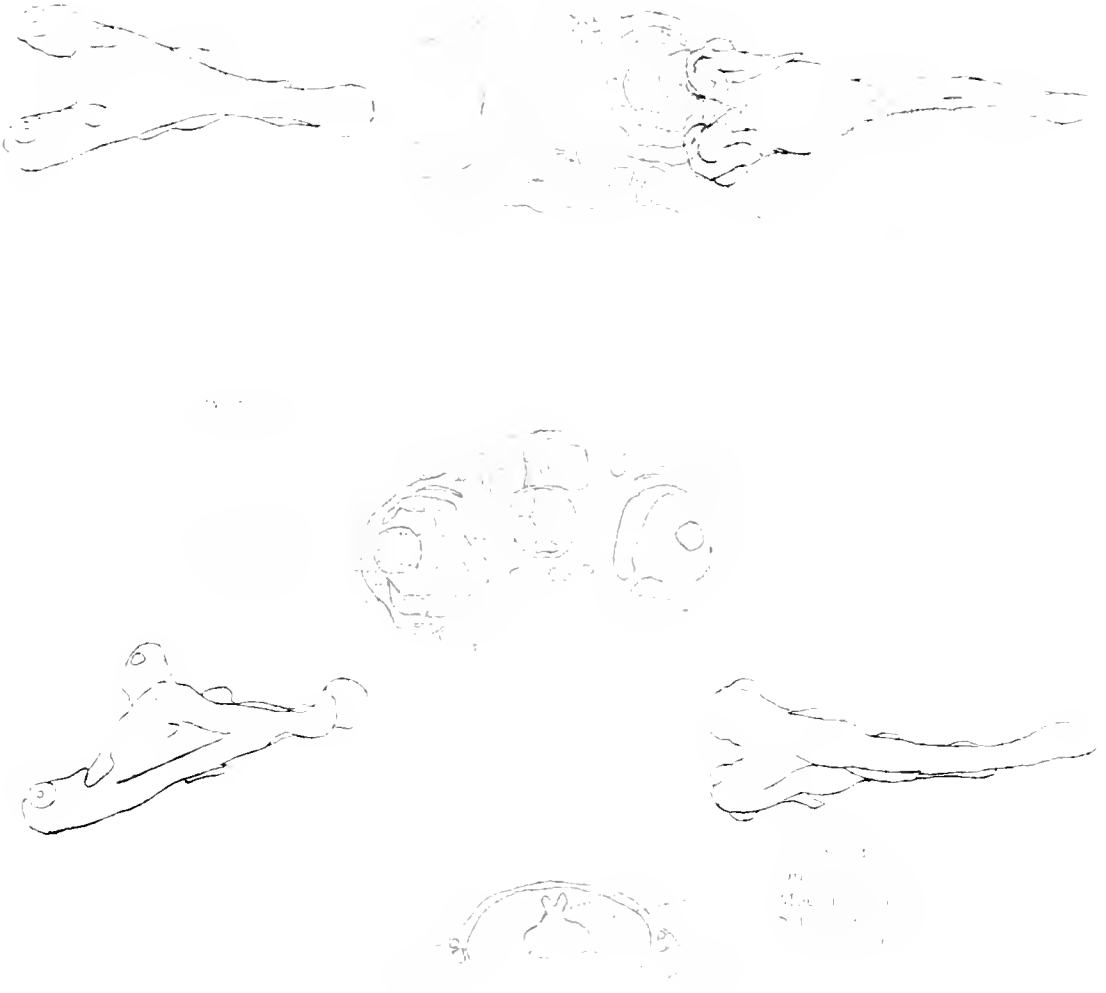
FIG. 10.—Double monster with union in posterior part of body. The union is obliquely by the ventral aspect of each twin, and the tail has three angles. See pp. 21-22. Compare Pl. VI. figs. 27 29, and Pl. VII. fig. 31. (× 3.)

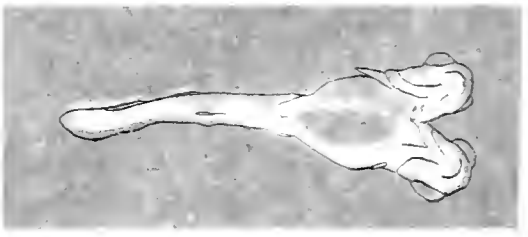
FIG. 8.—View from above of double monster, with union in pectoral region, the adjacent pectoral fins not being represented. For references see under Fig. 7. (× 3)

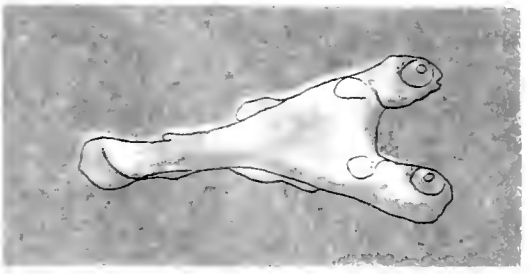
FIG. 11.—Double monster with union by posterior part of body. The tail is irregular, but resembles that of the preceding specimen. One of the twin heads is smaller than the other, and shows the condition of cyclopia. See pp. 7, 40 and Pl. XXIV. figs. 100-104, also Pl. XXV. figs. 107, 108. (× 3.)

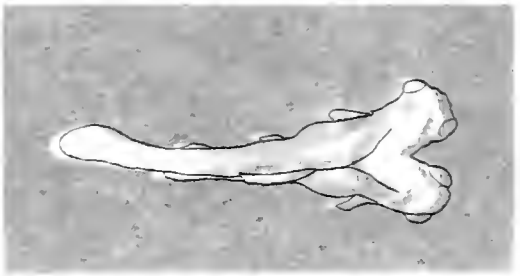
FIG. 9.—View from the side of a double monster, with union behind the pectoral region. One of the twins is much reduced in size. The posterior part of the body is single and symmetrical. For description see under Class V. on pp. 20-21. (× 3.)

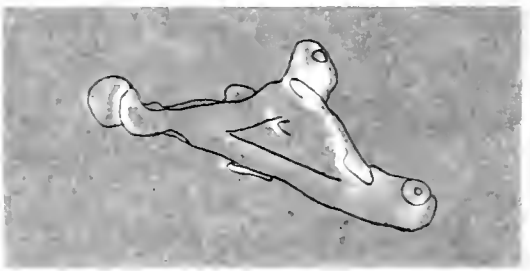
FIG. 12.—Double monster with symmetrical ventral union of the posterior parts of the twin bodies. Two pairs of pelvic fins are present, each pair being made up of components derived from different twins. The tail has four angles as in the section shown in Pl. VII. fig. 30. Description under Class VI. (*b*) on pp. 22-23. (× 3.)

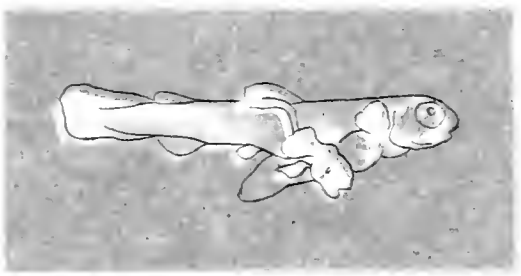


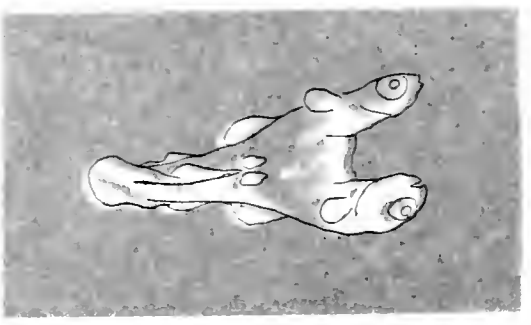


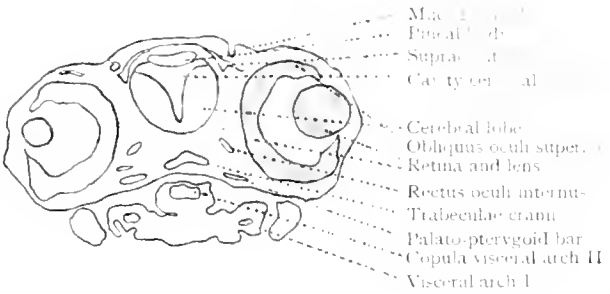


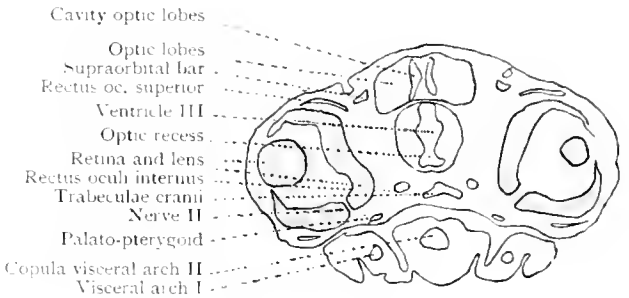


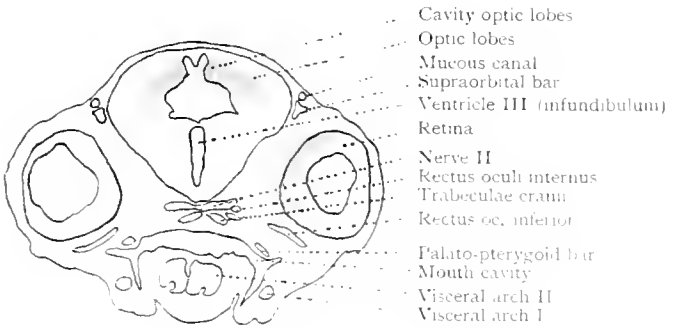


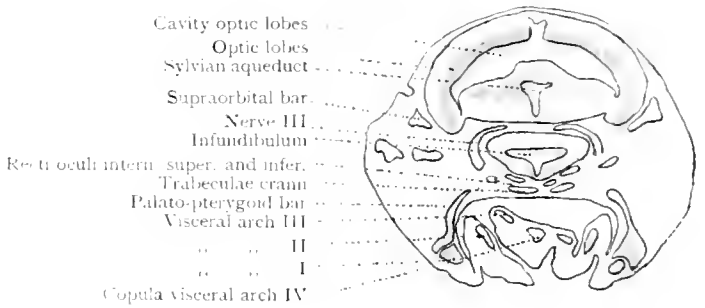


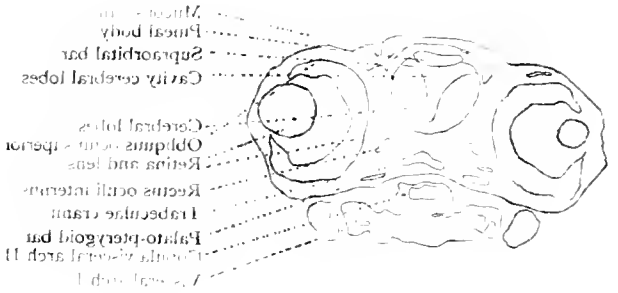


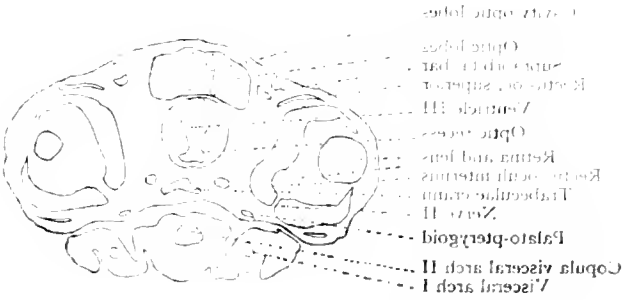

Cerebral lobe
Obliquus oculi super.
Retina and lens
Rectus oculi interna
Trabeculae cranii
Palato-pterygoid bar
Copula visceral arch II
Visceral arch I

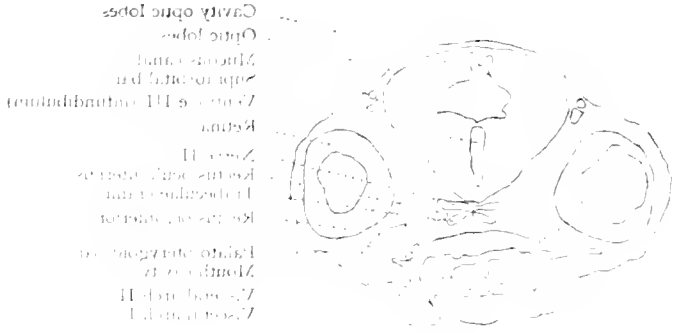

Cavity optic lobes
Optic lobes
Supraorbital bar
Rectus oc. superior
Ventricle III
Optic recess
Retina and lens
Rectus oculi internus
Trabeculae cranii
Nerve II
Palato-pterygoid
Copula visceral arch II
Visceral arch I

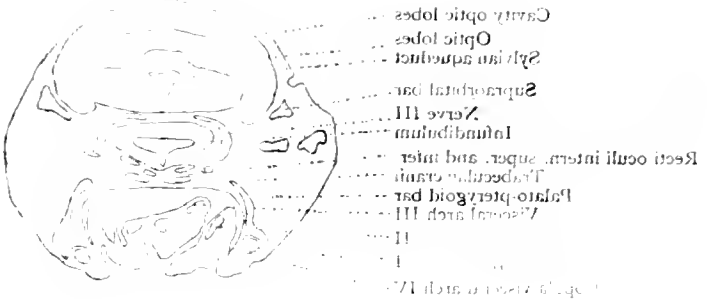

Cavity optic lobes
Optic lobes
Mucous canal
Supraorbital bar
Ventricle III (infundibulum)
Retina
Nerve II
Rectus oculi internus
Trabeculae cranii
Rectus oc. inferior
Palato-pterygoid bar
Mouth cavity
Visceral arch II
Visceral arch I


Cavity optic lobes
Optic lobes
Sylvian aqueduct
Supraorbital bar
Nerve III
Infundibulum
Trabeculae cranii
Palato-pterygoid bar
Visceral arch III
Copula visceral arch IV


Cavity cerebral lobes
Supraorbital bar
Pineal body
Palato-pterygoid bar
Trabeculae cranii
Retina and lens
Cerebral lobes


Optic lobes
Nerve III
Palato-pterygoid
Copula visceral arch II
Visceral arch I


Cavity optic lobes
Optic lobes
Nerve III
Retina


Cavity optic lobes
Optic lobes
Supraorbital bar
Nerve III
Trabeculae cranii

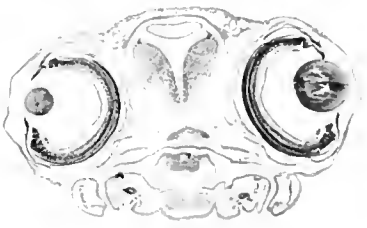


FIG. 13.—Transverse section through head of normal trout embryo (Pl. I. fig. 1), showing eyes, cerebral lobes, and pineal sac. Compare with Pl. VIII. fig. 35 (union at optic lobes) and Pl. XIII. fig. 47 (union at medulla). For other references see under Pl. I. fig. 1. (× 15.)

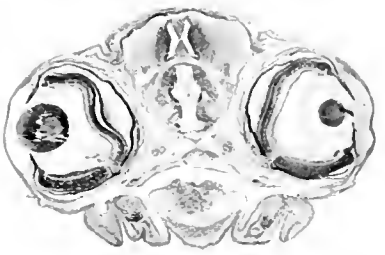


FIG. 14.—Transverse section through head of normal embryo (as in last figure), across anterior part of optic lobes and entrances of optic nerves. Compare with Pl. VIII. fig. 36 (union at optic lobes), and with Pl. XIV. fig. 50 (union at medulla). For other references see under Pl. I. fig. 1. (× 15.)

FIG. 15.—Transverse section as above, through middle of optic lobes and through optic commissure. For other references see under Pl. I. fig. 1. (× 15.)

FIG. 16.—Transverse section above, through back part of optic lobes and infundibulum. Compare with Pl. IX. fig. 37 (union at optic lobes), and with Pl. XIV. fig. 50 (union at medulla). For other references see under Pl. I. fig. 1. (× 15.)

FIG. 17. — Transverse section through head of normal trout embryo, showing cerebellum, auditory organs, medulla, pharynx, gill chambers, etc. Compare with Pl. XIV. fig. 51 (union at medulla). For other references see under Pl. I. fig. 1. (× 15.)

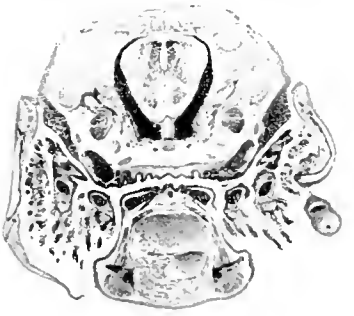


FIG. 18. Transverse section through head of normal trout embryo, showing the posterior part of the medulla, the gill chambers, and the anterior part of the heart. Compare with Pl. IX. fig. 38 (union at optic lobes). For other references see under Pl. I. fig. 1. (× 15.)

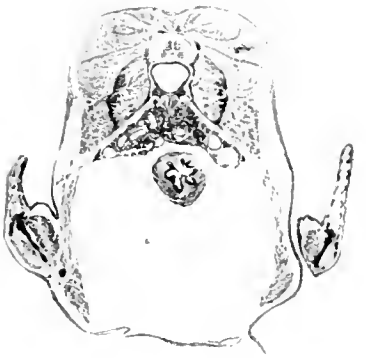
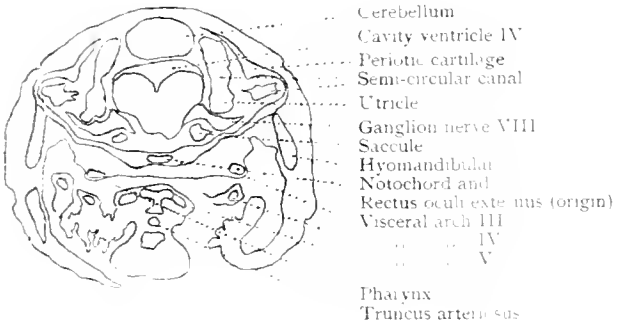
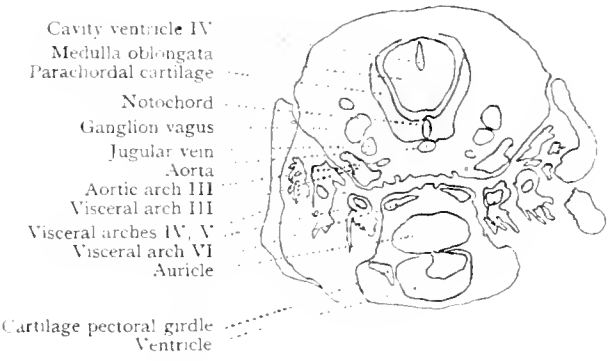
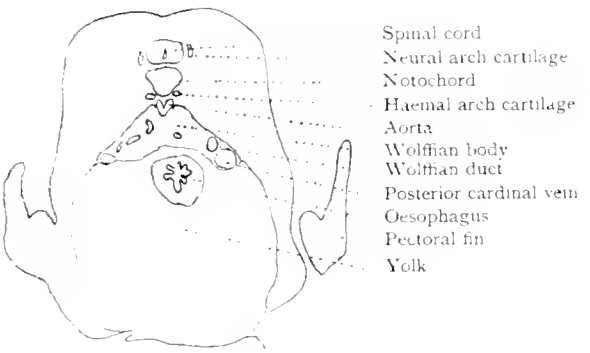


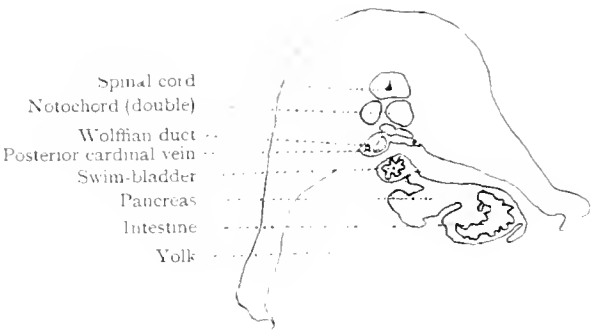
FIG. 19. — Transverse section of normal trout embryo in pectoral region. The section passes through the head-kidney, œsophagus, and pectoral fin. Other references under Pl. I. fig. 1. (× 15.)

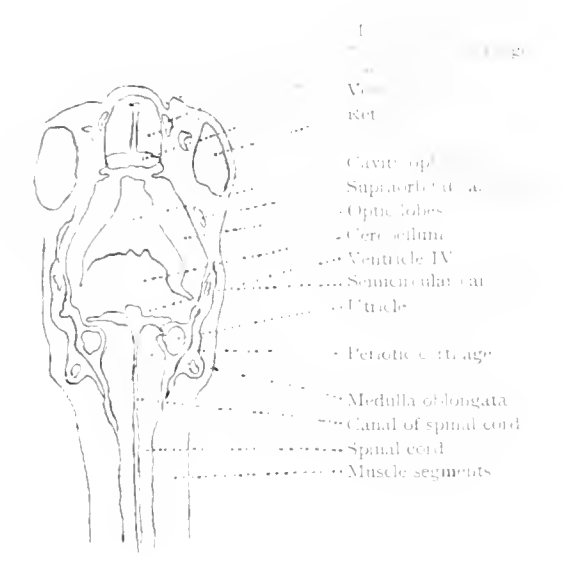
FIG. 20. — Transverse section of normal trout embryo, across middle of body, showing swim-bladder, intestine, and pancreatic tissue. The specimen, which is otherwise normal, shows local reduplication of the notochord. See p. 54. Other references under Pl. I. fig. 1. (× 15.)

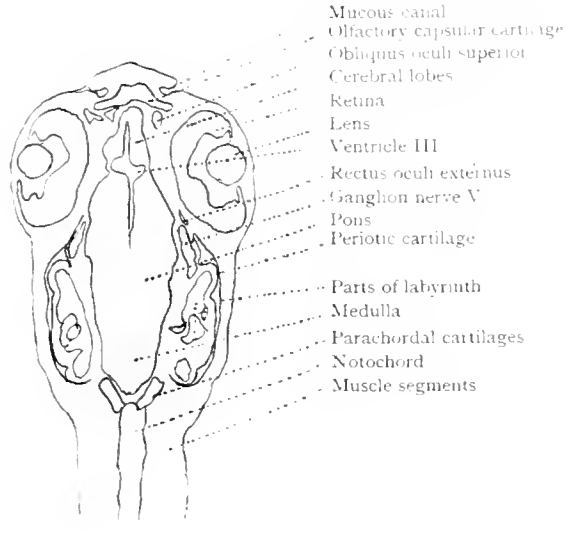

Cerebellum
Cavity ventricle IV
Periotic cartilage
Semi-circular canal
Utricle
Ganglion nerve VIII
Saccule
Hyomandibular
Notochord and
Rectus oculi externus (origin)
Visceral arch III
IV
V
Pharynx
Truncus arteriosus


Cavity ventricle IV
Medulla oblongata
Parachordal cartilage
Notochord
Ganglion vagus
Jugular vein
Aorta
Aortic arch III
Visceral arch III
Visceral arches IV, V
Visceral arch VI
Auricle
Cartilage pectoral girdle
Ventricle


Spinal cord
Neural arch cartilage
Notochord
Haemal arch cartilage
Aorta
Wolffian body
Wolffian duct
Posterior cardinal vein
Oesophagus
Pectoral fin
Yolk


Spinal cord
Notochord (double)
Wolffian duct
Posterior cardinal vein
Swim-bladder
Pancreas
Intestine
Yolk


Ret
Optic lobes
Cerebellum
Ventricle IV
Medulla oblongata
Canal of spinal cord
Spinal cord
Muscle segments


Mucous canal
Olfactory capsular cartilage
Obliquus oculi superior
Cerebral lobes
Retina
Lens
Ventricle III
Rectus oculi externus
Ganglion nerve V
Pons
Periotic cartilage
Parts of labyrinth
Medulla
Parachordal cartilages
Notochord
Muscle segments

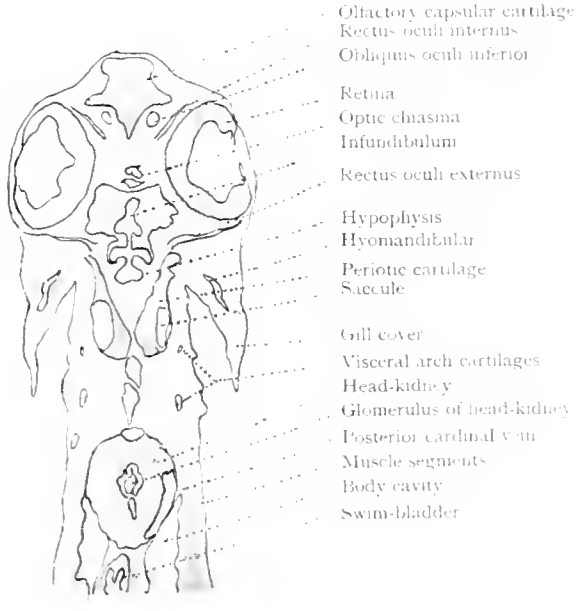

Olfactory capsular cartilage
Rectus oculi internus
Obliquus oculi inferior
Retina
Optic chiasma
Infundibulum
Rectus oculi externus
Hypophysis
Hyomandibular
Periotic cartilage
Saccule
Gill cover
Visceral arch cartilages
Head-kidney
Glomerulus of head-kidney
Posterior cardinal vein
Muscle segments
Body cavity
Swim-bladder

Fig. 21.—Horizontal section of normal trout embryo (Pl. I. fig. 1). The section passes through the upper parts of the eyes, and the auditory organs, as well as through the various cavities of the brain, and the central canal of the spinal cord. Compare with Pl. X. figs. 39, 40 (union at optic lobes), XII. fig. 43 (union at medulla), and with Pl. XV. fig. 53 (union in pectoral region). For other references see under Pl. I. fig. 1. (× 13.)

Fig. 22. Horizontal section as above, but passing below the cavities of the optic lobes and the medulla, and cutting through the middle of the eyes and the auditory organs. Compare with Pl. XII. figs. 44, 45 (union at medulla). Other references under Pl. I. fig. 1. (× 13.)

Fig. 23.—Horizontal section as above, but passing through the lower parts of the eyes, brain, and auditory organs, as well as through the head-kidney, the duct of the swim-bladder, and the dorsal portions of the gill arches, and of the body cavity. Compare with Pls. XI., XII. figs. 42, 45, 49 (union at optic lobes, and at medulla). Other references under Pl. I. fig. 1. (× 13.)

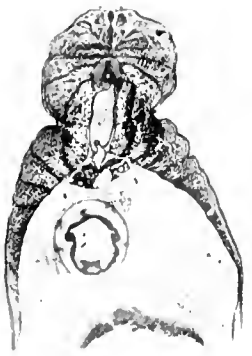


FIG. 24. — Transverse section through normal trout embryo, a considerable distance in front of the vent. Compare with Fig. 27 (union by posterior part of body). Other references under Pl. I. fig. 1. (× 14)

FIG. 27. — Transverse section corresponding with Fig. 24, but through a double monster of the type illustrated in Pl. II. fig. 10. Figs. 28, 29, and 31 are from the same series. At this level the two intestinal canals are widely separated. For relations of Wolffian ducts, etc., see pp. 22, 23 and Pl. XIX. figs 76-79. (× 14.)

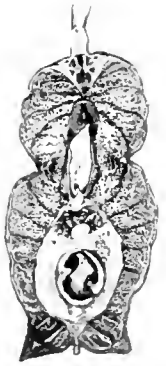
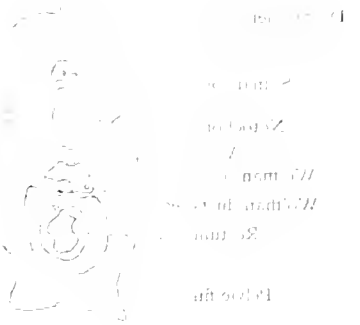


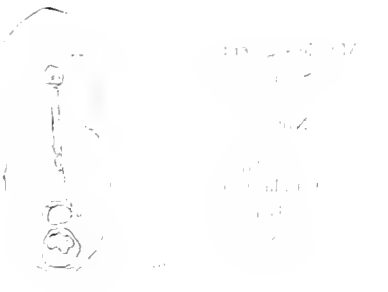
FIG. 25.—Transverse section as in Fig. 24, but a little further back. Compare with Fig. 28 (union by posterior part of body). Other references under Pl. I. fig. 1. (× 14)

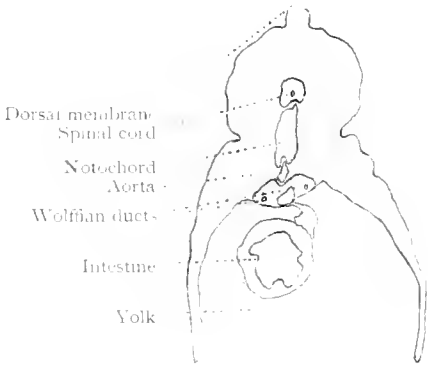
FIG. 28. — Transverse section of the same double monster as in Fig. 27, but a little further back in the series. The intestine is now single, but has two mesenteries. The Wolffian bodies and ducts are coming together by their inner, or adjacent, sides. Compare with Fig. 25 (normal). Other references under Fig. 27. (× 14.)

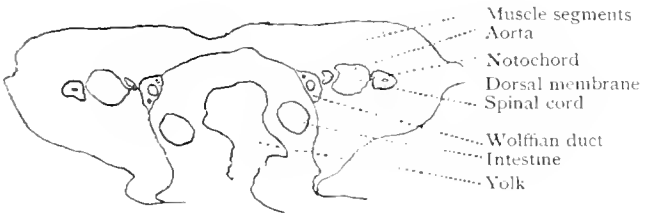
FIG. 26. — Transverse section, as in the two preceding figures, but passing just in front of the vent. The Wolffian ducts have opened into the bladder, which is seen lying dorsal to the rectum. Compare with Fig. 29 (union by posterior part of body). Other references under Pl. I. fig. 1. (× 14.)

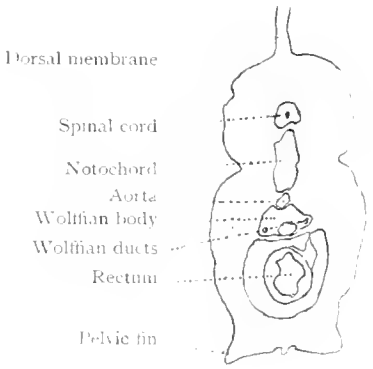
FIG. 29. — Transverse section through same double monster as in Figs. 27 and 28, but further back in the series. Compare with Fig. 26 (normal). The adjacent Wolffian ducts have opened into a first bladder, while the outer ducts have not yet reached the second one, which lies posterior to the other. These relations are explained on p. 23. Other references under Fig. 27. (× 14)

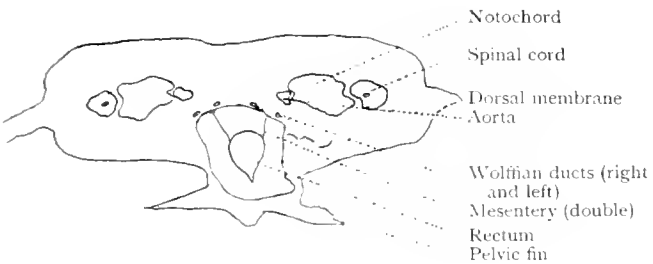


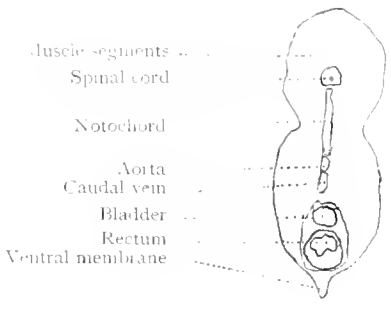


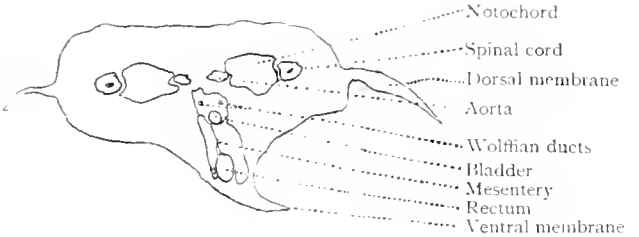

Dorsal membrane
Spinal cord
Notochord
Aorta
Wolffian ducts
Intestine
Yolk

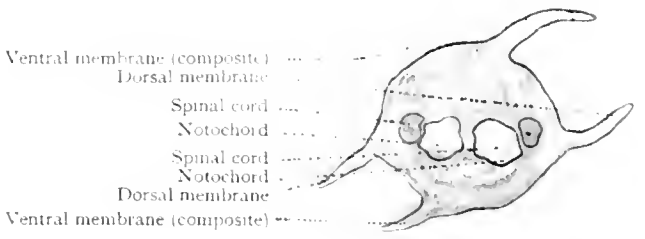

Muscle segments
Aorta
Notochord
Dorsal membrane
Spinal cord
Wolffian duct
Intestine
Yolk

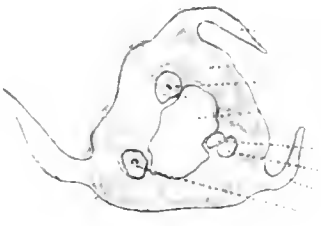

Dorsal membrane
Spinal cord
Notochord
Aorta
Wolffian body
Wolffian ducts
Rectum
Pelvic fin

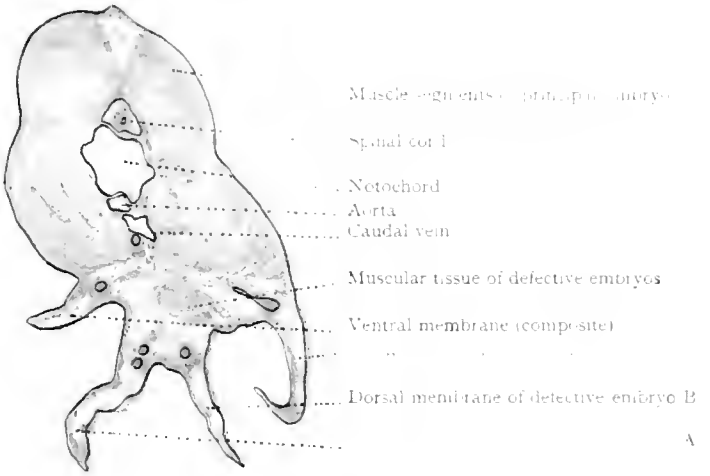

Notochord
Spinal cord
Dorsal membrane
Aorta
Wolffian ducts (right and left)
Mesentery (double)
Rectum
Pelvic fin

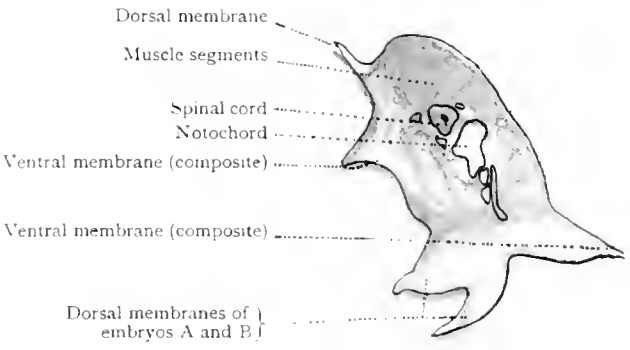

Muscle segments
Spinal cord
Notochord
Aorta
Caudal vein
Bladder
Rectum
Ventral membrane

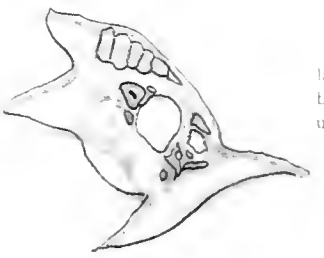

Notochord
Spinal cord
Dorsal membrane
Aorta
Wolffian ducts
Bladder
Mesentery
Rectum
Ventral membrane











Naming of parts same as in last figure. The dorsal membranes of A and B are now united.

Ventral membrane (composite)
Dorsal membrane
Spinal cord
Notochord
Spinal cord
Notochord
Dorsal membrane
Ventral membrane (composite)

Dorsal membrane
Muscle segments
Spinal cord
Notochord
Ventral membrane (composite)
Ventral membrane (composite)
Dorsal membranes of
embryos A and B

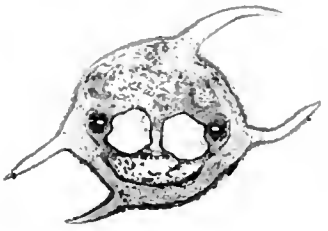


FIG. 30.—Transverse section through tail of embryo belonging to the type illustrated in Pl. II. fig. 12 (ventral union by posterior part of body). There are two spinal cords, notochords, and dorsal edge membranes. Two ventral edge membranes are also present, but these are composite, being derived from the widely separated halves of ventral membranes belonging to each of the twins. This is an example of almost pure ventral union. See pp. 22-23. Compare with Fig. 31. (× 14.)

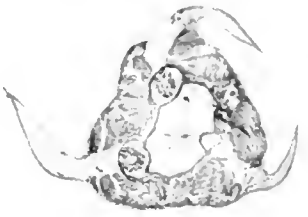
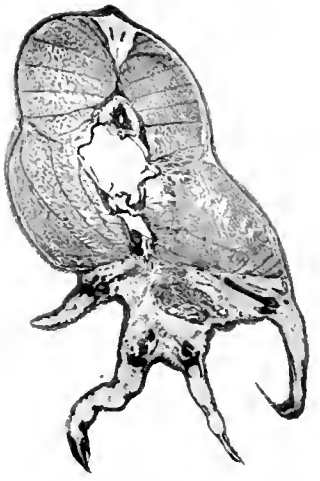


FIG. 31.—Transverse section through tail of an embryo belonging to the general type illustrated in Pl. VI. figs. 27-29. The two notochords have fused together, and the ventral edge membrane is composite and single. Compare with Fig. 30. See also under Fig. 27. (× 14.)

FIG. 32.—Transverse section through commencement of the tail of the triple monster trout described on pp. 33-34. See also Pl. XXII. figs. 94-96 and Pl. XXIII. figs. 97-99. The section is taken up chiefly with structures belonging to the principal embryo, but it shows also, near the middle line on the under aspect, the two dorsal fins of the defective embryos. A little further up on either side is a composite ventral edge membrane (anal fin), belonging in part to the principal embryo and in part to one or other of the defective embryos. (× 18.)



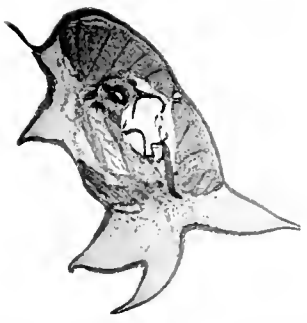


FIG. 33.—Transverse section through tail of same specimen as in last figure, but considerably further back. All the fin membranes are still present, but the two dorsals of the defective embryos have almost united. The section, as well as the succeeding one, may be compared with Figs. 30 and 31. Other references under Fig. 32. (× 18.)

FIG. 34.—Transverse section as above. The dorsal fins of the defective embryos have now united. (× 18.)

FIG. 35.—Transverse section through anterior part of head of a double monster belonging to Class I., the type illustrated in Pl. I. figs. 4 and 5. The posterior walls of the adjacent eyes are just grazed by the section, and several of the ocular nerves and muscles are seen. The cerebral lobes and their cavity, the pineal sacs, and a forwardly projecting part of the composite optic lobes come into the section. Noticeable in the middle line, ventrally, is a large cartilage consisting of the fused adjacent hyomandibulars, with which articulates a small bar representing the adjacent Meckelian cartilages. Compare with Pl. III. fig. 13 (normal) and with Pl. XIII. fig. 48 (union at medulla). Pls. X.–XII. figs. 30-46 are also from sections of a double monster similar to this one, *i.e.* with union at optic lobes. For plane of section see Pl. XXI. figs. 88-90. Other references are given under Pl. I. fig. 4. (× 20.)

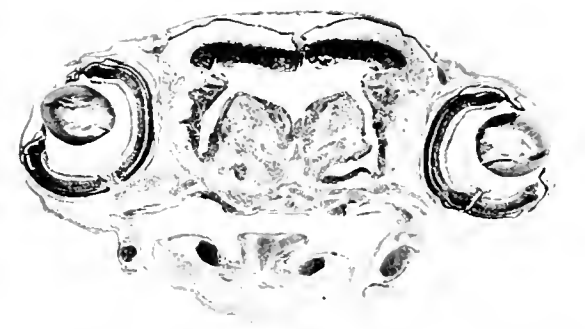
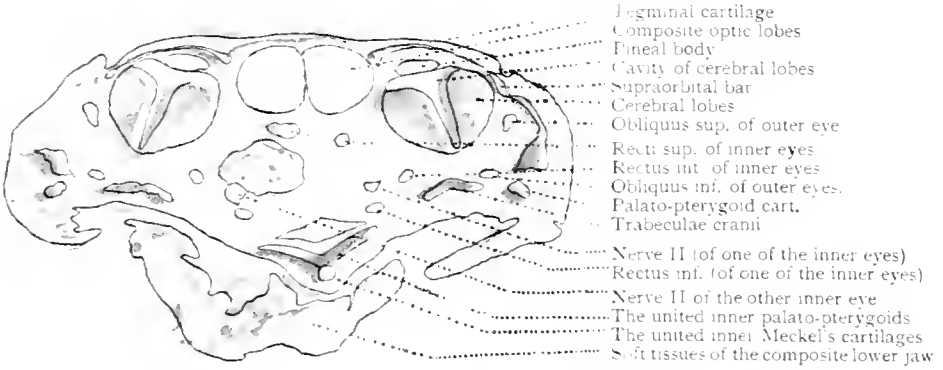
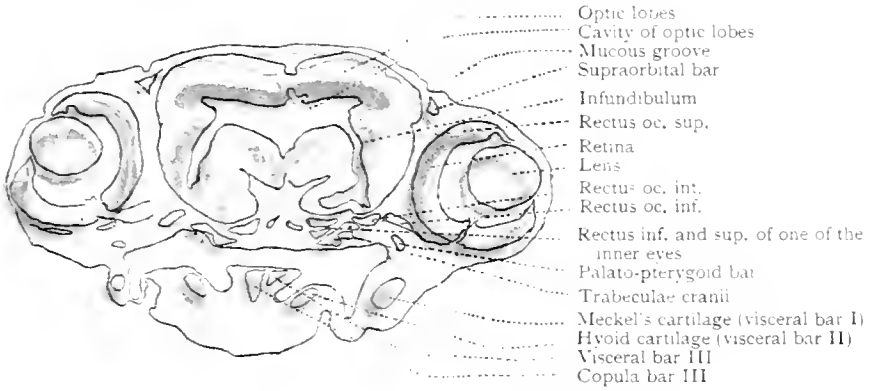


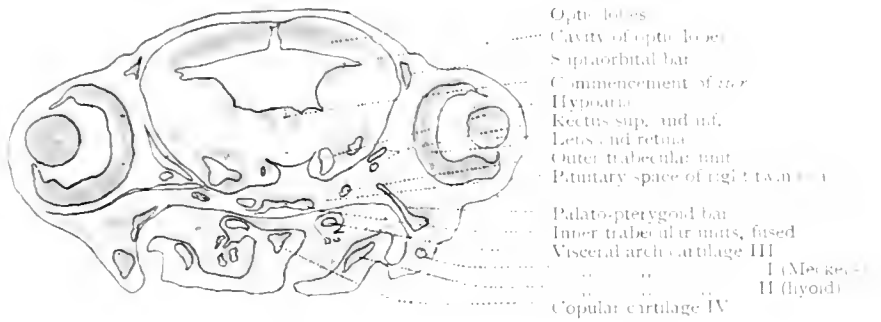
FIG. 36.—Transverse section from same series as Fig. 35, but passing across the middle of the outer eyes. There are two infundibula, but the composite optic lobe region has a single cavity. The trabeculae cranii are doubled. A few of the muscles belonging to the adjacent eyes are cut across near their origins. In the floor of the mouth, the two first visceral arch bars and the copula of the third are seen. Compare with Pl. III. figs. 14 and 15 (normal). For other references see under Pl. I. fig. 4, and for plane of section see Pl. XXI. figs. 88-90, line 30. (× 20.)

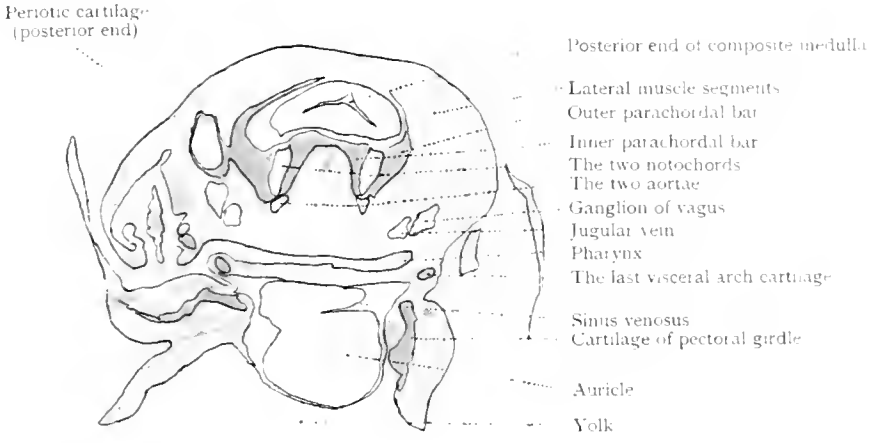
Terminal cartilage
Composite optic lobes
Pineal body
Cavity of cerebral lobes
Supraorbital bar
Cerebral lobes
Obliquus sup. of outer eye
Recti sup. of inner eyes
Rectus int. of inner eyes
Obliquus int. of outer eyes
Palato-pterygoid cart.
Trabeculae cranii
Nerve II (of one of the inner eyes)
Rectus int. (of one of the inner eyes)
Nerve II of the other inner eye
The united inner palato-pterygoids
The united inner Meckel's cartilages
Soft tissues of the composite lower jaw

Optic lobes
Cavity of optic lobes
Mucous groove
Supraorbital bar
Retina
Lens
Rectus oc. inf.
Rectus oc. inf. and sup. of one of the inner eyes
Trabeculae cranii
Meckel's cartilage (visceral bar I)
Hyoid cartilage (visceral bar II)
Visceral bar III
Copula bar III


Tegminal cartilage
Composite optic lobes
Pineal body
Cavity of cerebral lobes
Supraorbital bar
Cerebral lobes
Obliquus sup. of outer eye
Recti sup. of inner eyes
Rectus int. of inner eyes
Obliquus inf. of outer eyes.
Palato-pterygoid cart.
Trabeculae cranii
Nerve II (of one of the inner eyes)
Rectus inf. (of one of the inner eyes)
Nerve II of the other inner eye
The united inner palato-pterygoids
The united inner Meckel's cartilages
Soft tissues of the composite lower jaw


Optic lobes
Cavity of optic lobes
Mucous groove
Supraorbital bar
Infundibulum
Rectus oc. sup.
Retina
Lens
Rectus oc. int.
Rectus oc. inf.
Rectus inf. and sup. of one of the inner eyes
Palato-pterygoid bar
Trabeculae cranii
Meckel's cartilage (visceral bar I)
Hyoid cartilage (visceral bar II)
Visceral bar III
Copula bar III


Optic lobes
Cavity of optic lobes
Supraorbital bar
Commencement of iter
Hypoaria
Rectus sup. and inf.
Lens and retina
Outer trabecular unit
Pituitary space of right twin area
Palato-pterygoid bar
Inner trabecular units, fused
Visceral arch cartilage III
" " I (Meckel's)
" " " II (hyoid)
Copular cartilage IV


Periotic cartilage
(posterior end)
Posterior end of composite medulla
Lateral muscle segments
Outer parachordal bar
Inner parachordal bar
The two notochords
The two aortae
Ganglion of vagus
Jugular vein
Pharynx
The last visceral arch cartilage
Sinus venosus
Cartilage of pectoral girdle
Auricle
Yolk

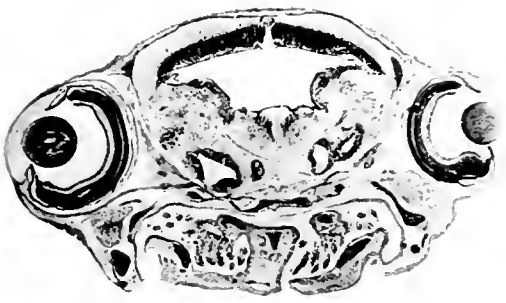


FIG. 37.—Transverse section from same series (double monster with union at optic lobes) as that illustrated in the two preceding figures. The section is further back than in Fig. 36. Evidences of duplicity are disappearing, but some are still to be made out, *e.g.* two sets of infundibular downgrowths in the floor of the brain, and two pairs of trabeculae, of which the inner, or adjacent, units have united to form a mesial bar separating the two pituitary spaces. Compare with Pl. III. fig. 16 (normal) and with Pl. XIV. fig. 50 (union at medulla). Other references under Pl. I. fig. 4 and plane of section in Pl. XXI. figs. 88-90, line 37. (· 20.)

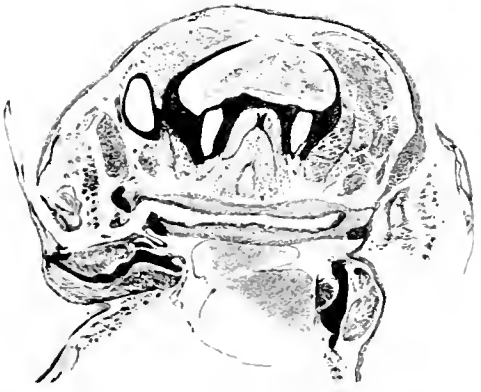


FIG. 38.—Transverse section from same series as in the last three figures, but passing through the back part of the head. It is remarkable that the evidence of duplicity here is greater than in the preceding section. The two notochords are widely separated, and are surrounded by a mass of cartilage representing both pairs of parachordals. There is a median series of muscle segments representing the fused adjacent somites. The heart cavities, however, form a single series. Compare with Pl. IV. fig. 18 (normal) and with Pl. XVII. fig. 57 (union at medulla). Other references under Pl. I. fig. 4, and plane of section in Pl. XXI. figs. 88-90, line 38. (· 20.)

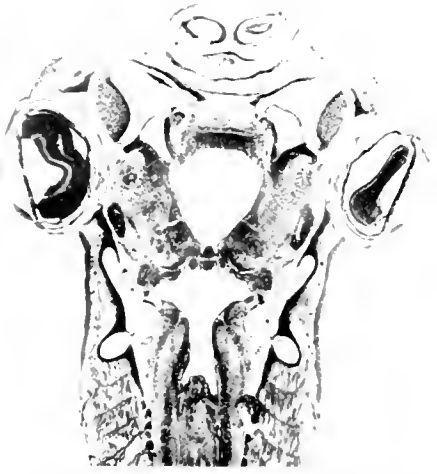
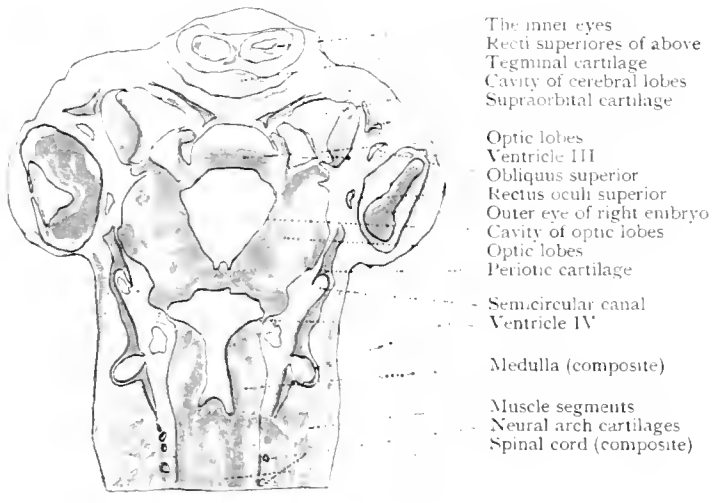


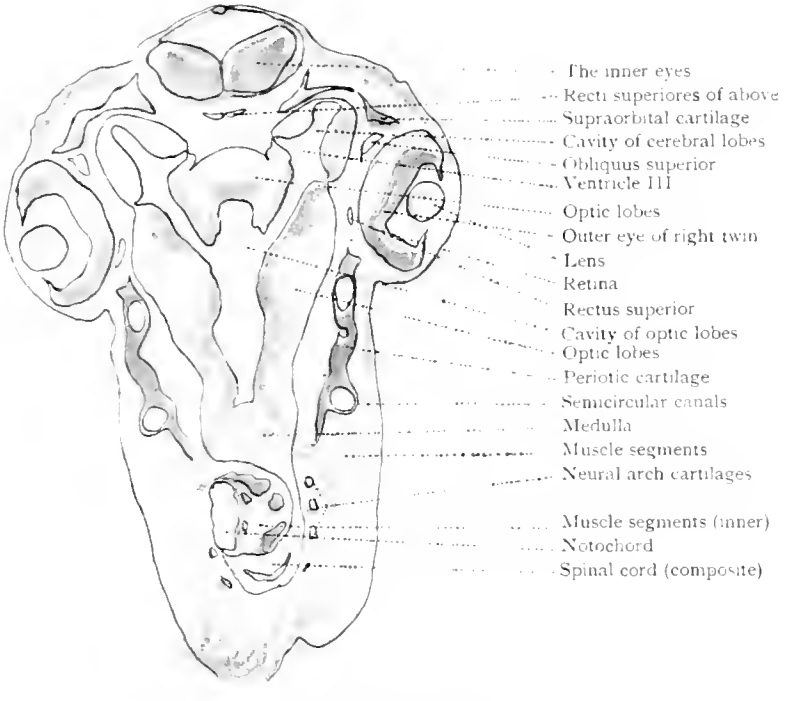
FIG. 39. Horizontal section through a double monster with union in region of optic lobes, and belonging to Class I., *i.e.* the type illustrated in Pl. I. figs. 4-5 (surface views), and in Pls. VIII.-IX. figs. 35-38 (transverse sections). Compare with Pl. V. fig. 21 (section of a normal embryo at the corresponding level). The section passes through the upper parts of all four eyes of the two auditory organs. The two forebrains are cut somewhat obliquely, while the large composite optic lobes and their central cavity are seen in horizontal section, as also are the fourth ventricle and the medulla oblongata. Other references are given under Pl. I. fig. 4. (× 16.)

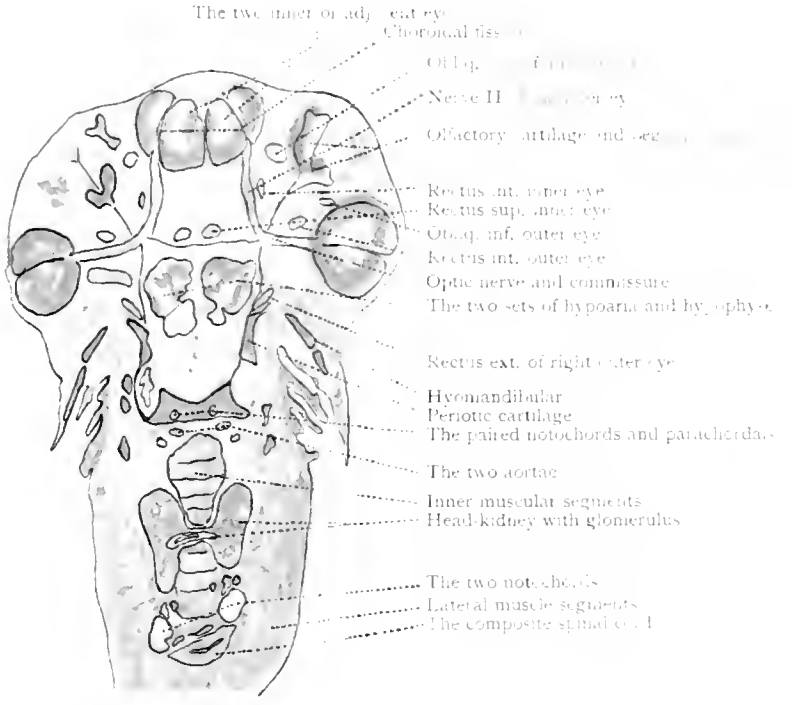
FIG. 40. Horizontal section of the same double monster as in last figure, but at a slightly deeper level. The section passes through the middle of the outer eyes, but only through the upper segments of the adjacent eyes. The composite cavity of the optic lobes will be seen to bifurcate in front, and lead into the cavities of the two forebrains. For other references see under Pl. I. fig. 4. (× 16.)

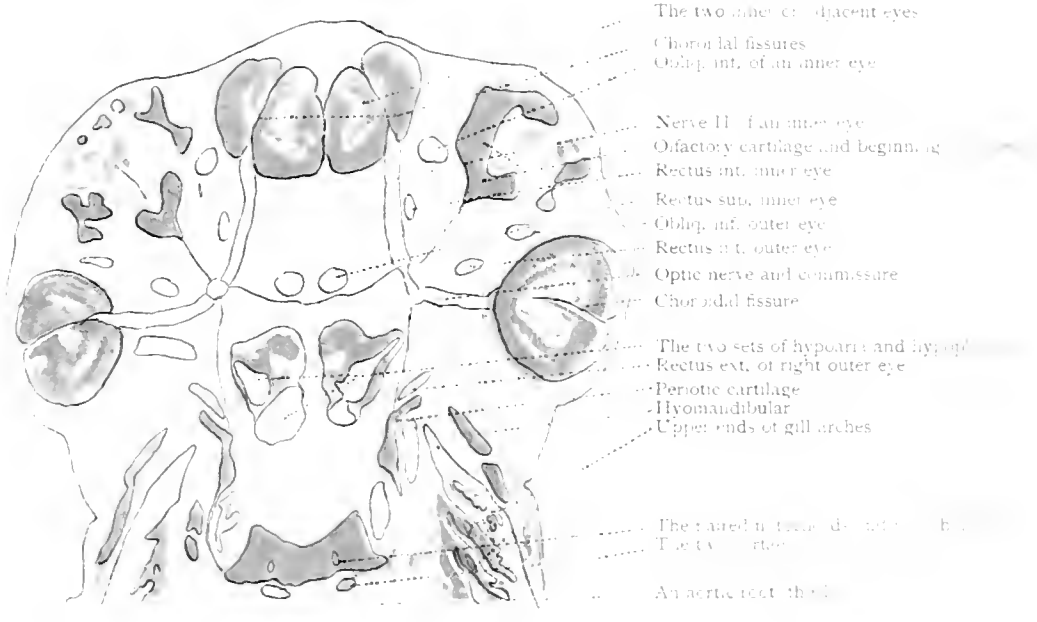
The inner eyes
Nasal capsules or above
Perinasal cartilage
Cavity of cerebral lobes
Supraorbital cartilage
Optic lobes
Ventricle III
Obliquus superior
Rectus oculi superior
Outer eye of right embryo
Cavity of optic lobes
Optic lobes
Periotic cartilage
Semicircular canal
Ventricle IV
Medulla (composite)
Muscle segments
Neural arch cartilages
Spinal cord (composite)

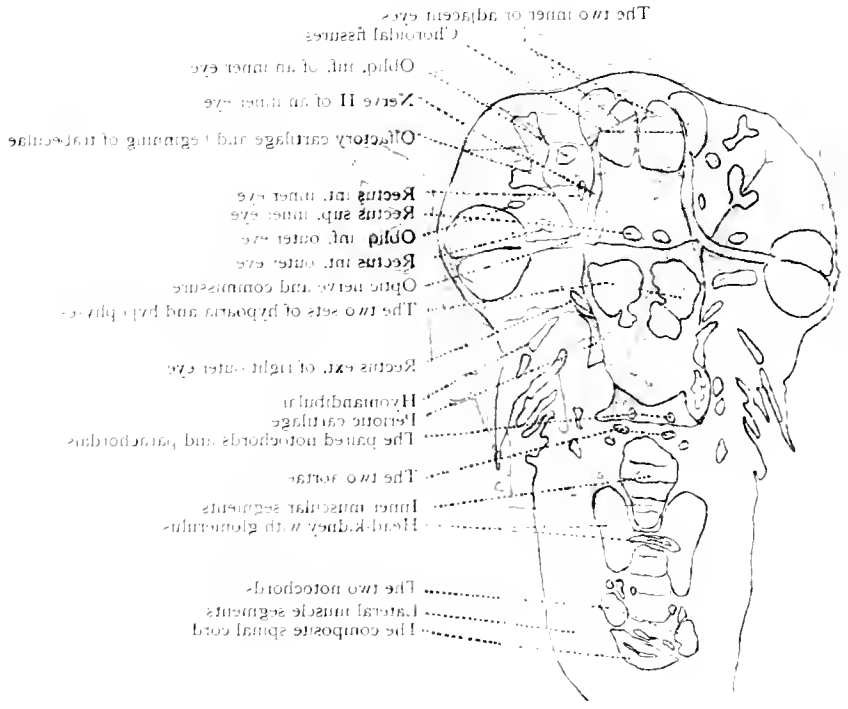
The inner eyes
Nasal capsules or above
Supraorbital cartilage
Cavity of cerebral lobes
Obliquus superior
Ventricle III
Optic lobes
Outer eye of right twin
Lens
Retina
Rectus superior
Cavity of optic lobes
Optic lobes
Periotic cartilage
Semicircular canals
Medulla
Muscle segments
Neural arch cartilages
Muscle segments (inner)
Notochord
Spinal cord (composite)


The inner eyes
Recti superiores of above
Tegminal cartilage
Cavity of cerebral lobes
Supraorbital cartilage
Optic lobes
Ventricle III
Obliquus superior
Rectus oculi superior
Outer eye of right embryo
Cavity of optic lobes
Optic lobes
Periotic cartilage
Semicircular canal
Ventricle IV
Medulla (composite)
Muscle segments
Neural arch cartilages
Spinal cord (composite)


The inner eyes
Recti superiores of above
Supraorbital cartilage
Cavity of cerebral lobes
Obliquus superior
Ventricle III
Optic lobes
Outer eye of right twin
Lens
Retina
Rectus superior
Cavity of optic lobes
Optic lobes
Periotic cartilage
Semicircular canals
Medulla
Muscle segments
Neural arch cartilages
Muscle segments (inner)
Notochord
Spinal cord (composite)


The two inner of adjacent eyes
Choroidal fissures
Obliq. inf. of an inner eye
Nerve II
Olfactory cartilage and beginning
Rectus int. inner eye
Rectus sup. inner eye
Obliq. inf. outer eye
Rectus int. outer eye
Optic nerve and commissure
The two sets of hypoarcs and hypophyses
Rectus ext. of right outer eye
Hyomandibular
Periotic cartilage
The paired notochords and parachordals
The two aortae
Inner muscular segments
Head-kidney with glomerulus
The two notochords
Lateral muscle segments
The composite spinal cord


The two inner of adjacent eyes
Choroidal fissures
Obliq. inf. of an inner eye
Nerve II
Olfactory cartilage and beginning
Rectus int. inner eye
Rectus sup. inner eye
Obliq. inf. outer eye
Rectus int. outer eye
Optic nerve and commissure
Choroidal fissure
The two sets of hypoarcs and hypophyses
Rectus ext. of right outer eye
Periotic cartilage
Hyomandibular
Upper ends of gill arches
The paired notochords
The two aortae
An aortic root


The two inner or adjacent eyes
Choroidal fissures
Oblq. inf. of an inner eye
Nerve II of an inner eye
Olfactory cartilage and beginning of trabeculae
Rectus sup. inner eye
Rectus inf. outer eye
Oblq. inf. outer eye
Rectus ext. outer eye
Optic nerve and commissure
The two sets of hypoura and hypophyses
Rectus ext. of right outer eye
Hyomandibular
Ptérotic cartilage
The paired notochords and paraboridus
The two aortae
Inner muscular segments
Head-kidney with glomerulus
The two notochords
Lateral muscle segments
The composite spinal cord

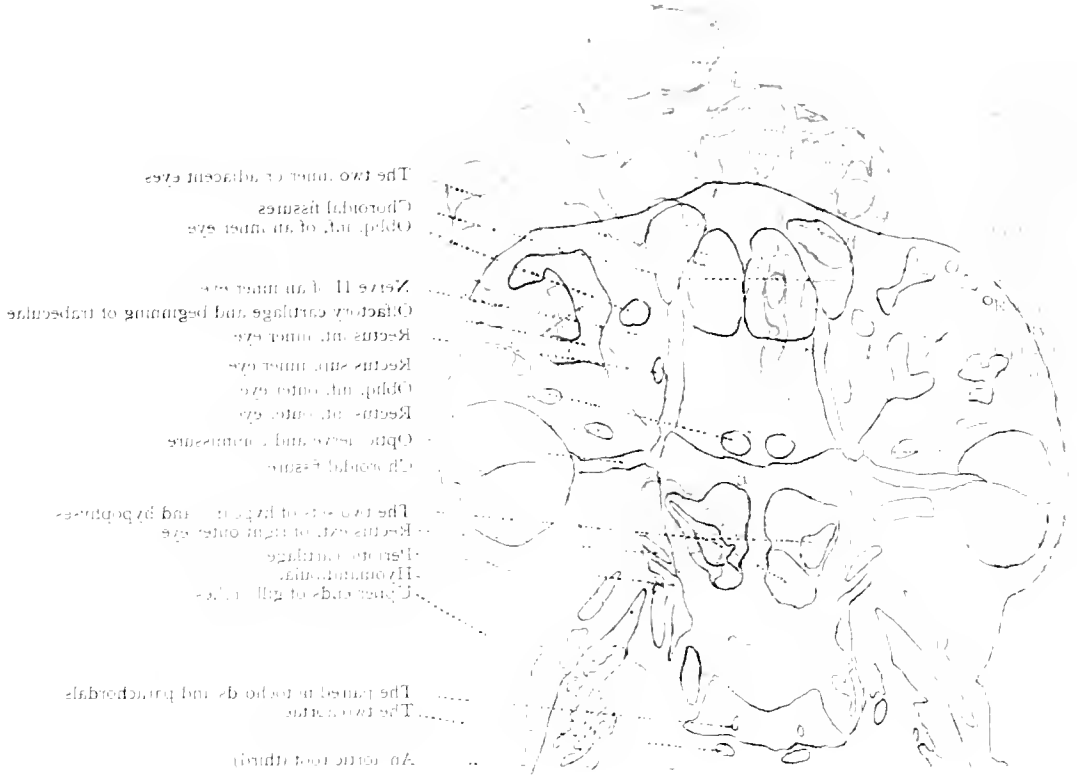

The two inner or adjacent eyes
Choroidal fissures
Oblq. inf. of an inner eye
Nerve II of an inner eye
Olfactory cartilage and beginning of trabeculae
Rectus sup. inner eye
Rectus sup. inner eye
Oblq. inf. outer eye
Rectus ext. outer eye
Optic nerve and commissure
Otic capsule fissure
The two sets of hypoura and hypophyses
Rectus ext. of right outer eye
Parotic cartilage
Hyomandibular
Spinal cords of gill arches
The paired notochords and paraboridus
The two aortae
An aortic roof arch

FIG. 41.—Horizontal section through same double monster as in last two figures. The section is at a still deeper level, and passes below the auditory organs, through the basal parts of the brain and the lower segments of the eyes. All four optic nerves and fissures are seen. Owing to the curvature of the specimen, the body is cut through somewhat obliquely, and shows the two notochords and head-kidneys, as well as the composite spinal cord and the median muscular mass. There is greater apparent duplicity in the forepart of the body than in the posterior cerebral region. For other references see under Pl. I. Fig. 1. (× 12.)

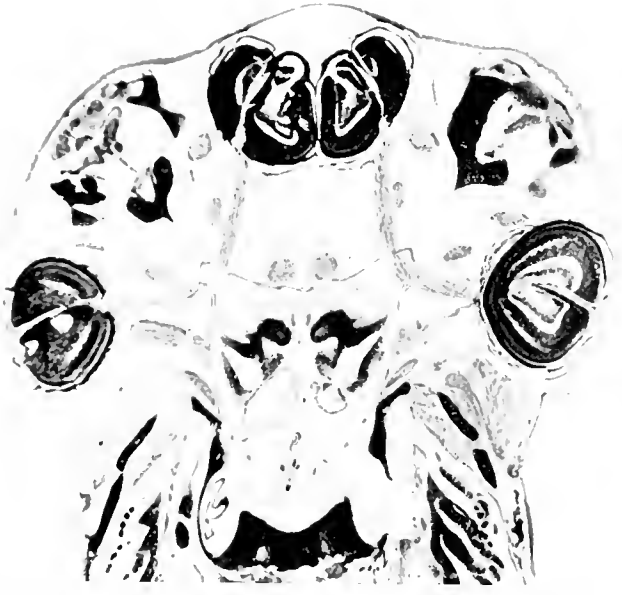


FIG. 42.—The anterior part of last specimen shown in higher magnification. (× 21.)

FIGS. 43-46.—Horizontal sections of double monster (union at optic lobes), belonging to the same type as the specimen illustrated in Pl. I. figs. 4, 5, Pls. VIII., IX. figs. 35-38, and Pls. X., XI. figs. 35-42. The moulding of the adjacent eyes and brain parts presents, however, some important differences when compared with the two last-named sets of figures. The eyes are turned towards one another, so that the common lens lies buried below the surface in the centre of the globe. The optic lobes show greater evidence of duplicity, as also do the parts round the *iter* and the fourth ventricle. Owing to curvature of the specimen, the body is cut through obliquely, as in Pls. X., XI. figs. 30-41, and shows a double condition of the notochord and of certain other structures. The gullet and rest of the alimentary canal are single, but there are two swim-bladders and air-ducts. For general references see under Pl. I. fig. 4.

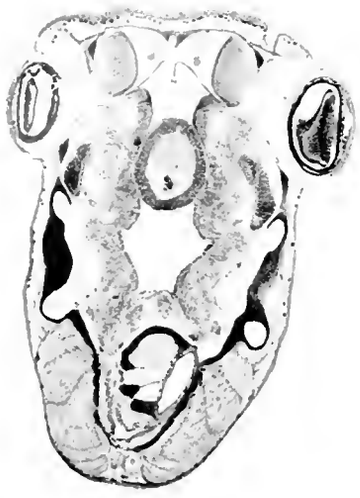


FIG. 43.—Horizontal section of the embryo described above, passing through upper parts of eyes, brain and auditory organs. The fused adjacent sides of the optic lobes form a rounded mass, projecting into the central cavity. Dorsally, the sagittal planes of the twin fore-brains are much inclined towards one another. (· 14.)

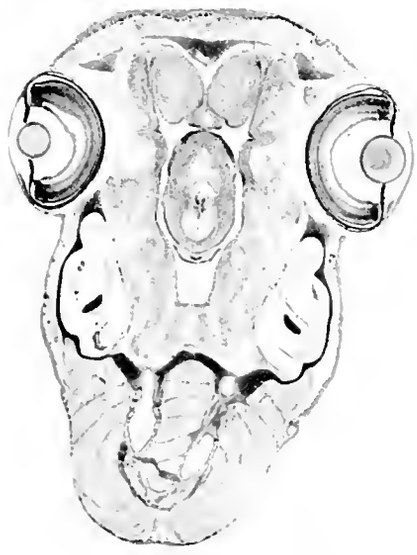


FIG. 44. Horizontal section of the embryo described above, passing through the middle of the outer eyes and of the auditory organs. The mesial optic lobe mass, referred to under Fig. 43, is now larger. The mesial muscular mass between the two notochords is also to be noted. (· 14.)

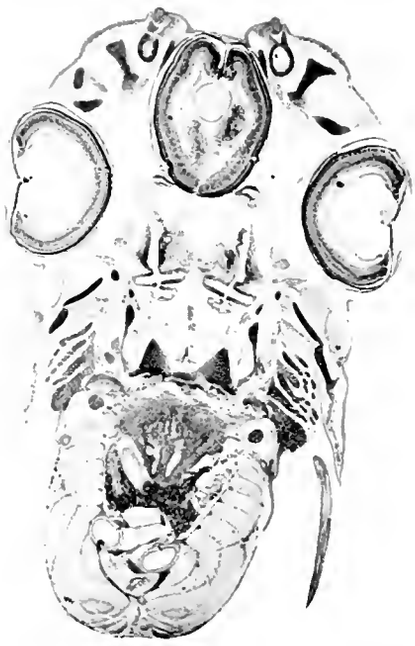
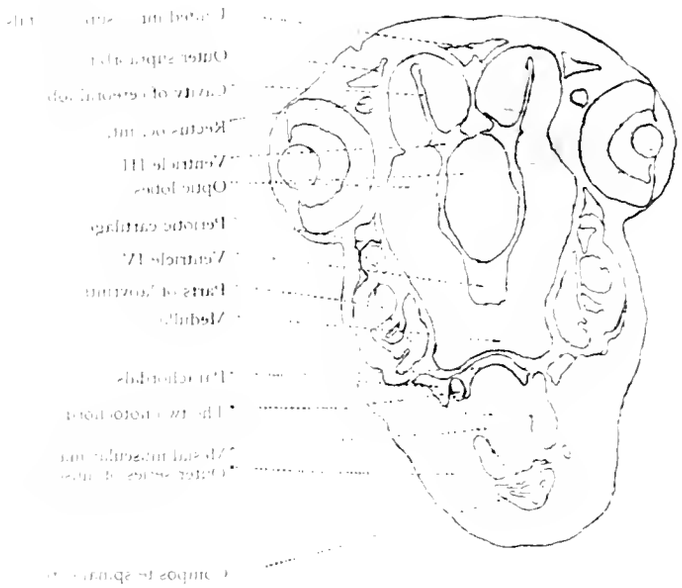
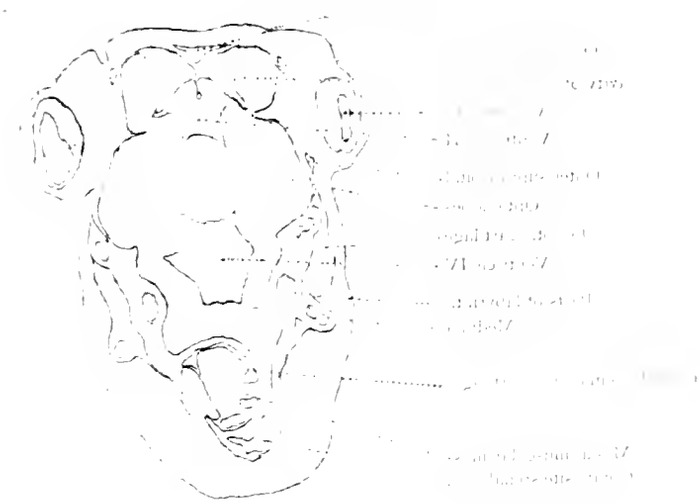
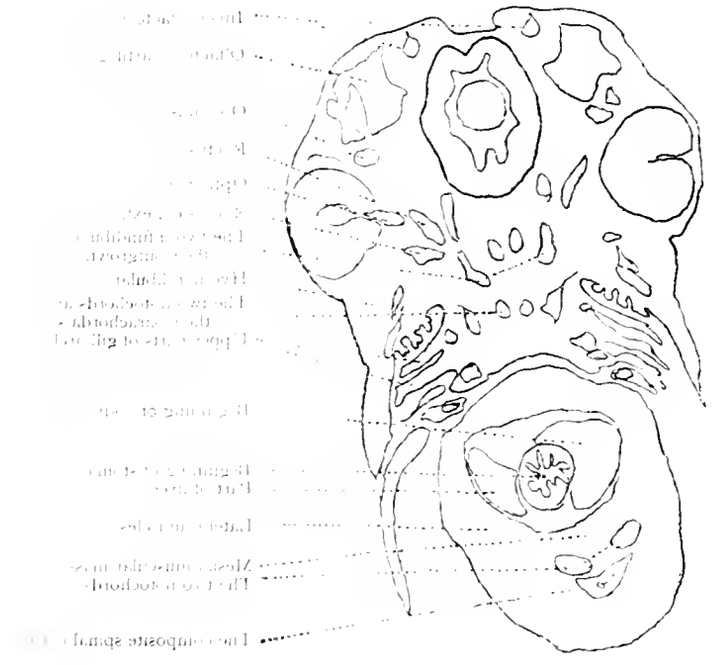


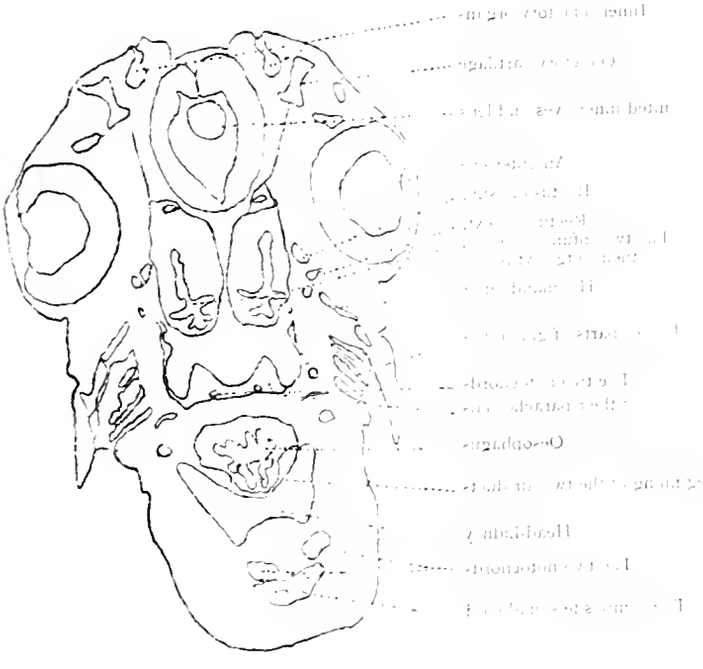
FIG. 45.—Horizontal section of the embryo described above, at a deeper level than in the last two figures. The adjacent olfactory pits and the two adjacent eyes with single lens in the middle of the globe are seen, as also are the two sets of infundibular outgrowths and the origins of the two swim-bladders. (· 14.)

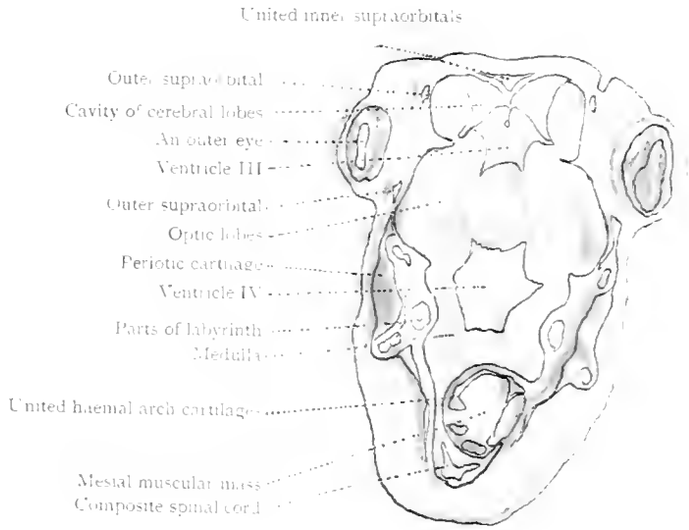
FIG. 46.—Horizontal section of the embryo described above, at a deeper level than in Fig. 45. The globe made up of the fused adjacent eyes is cut in median section, while the outer eyes show their choroidal fissure and places of entrance of the optic nerves. (· 14.)

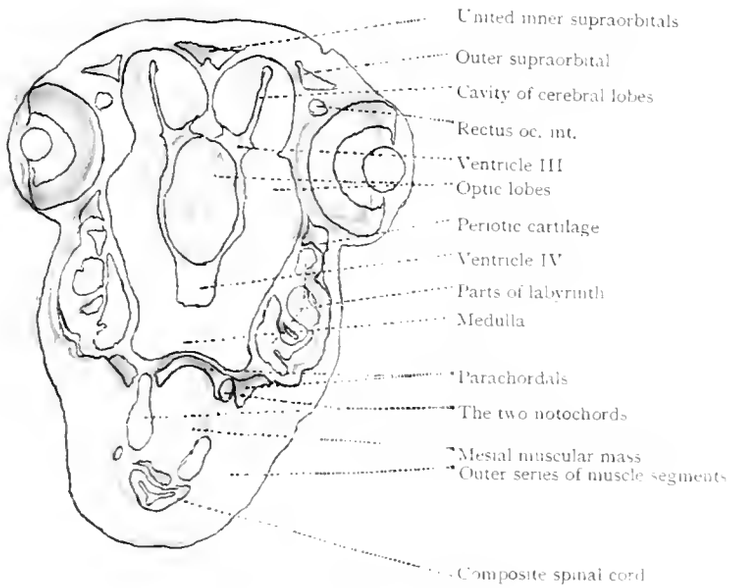


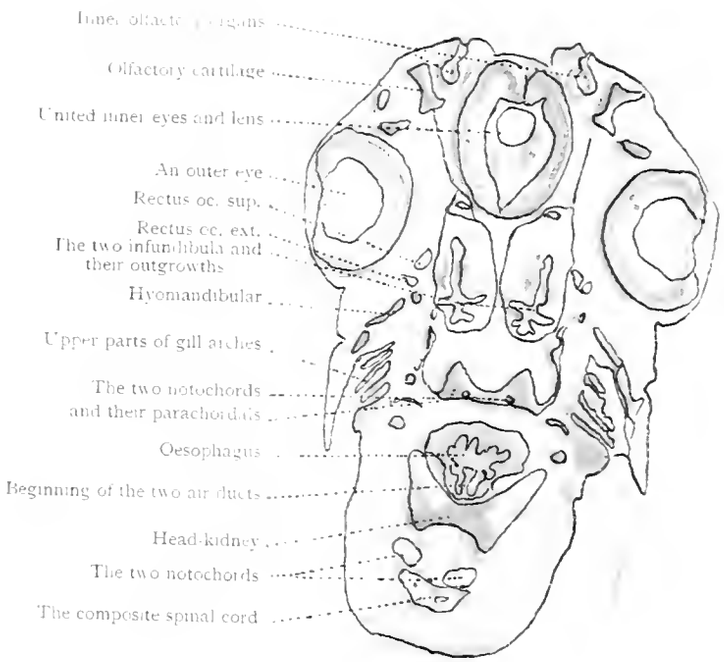


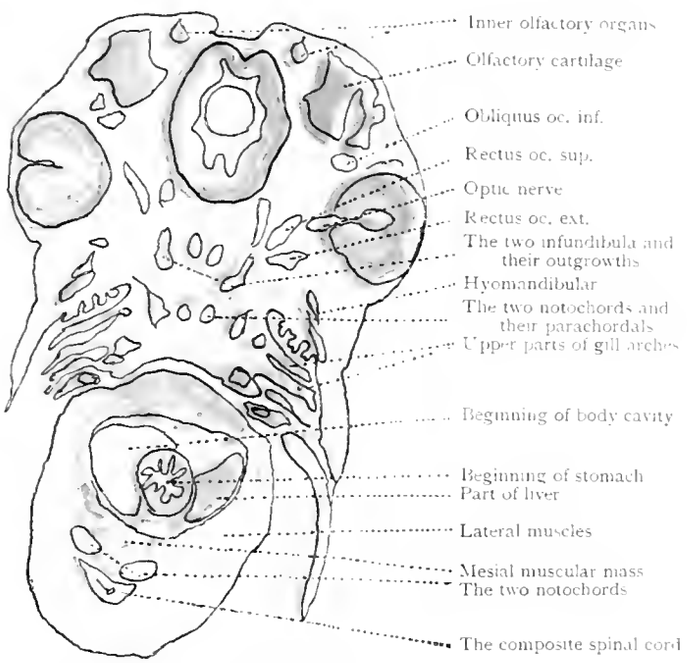


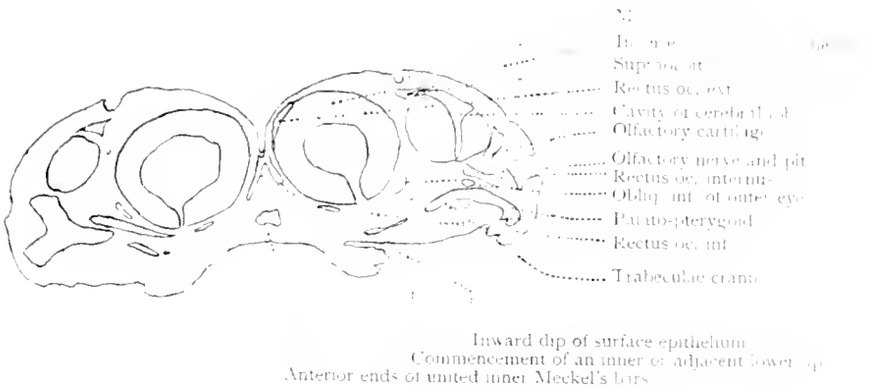



United inner supraorbitals
Outer supraorbital
Cavity of cerebral lobes
An outer eye
Ventricle III
Outer supraorbitals
Optic lobes
Periotic cartilage
Ventricle IV
Parts of labyrinth
Medulla
United haemal arch cartilage
Mesial muscular mass
Composite spinal cord


United inner supraorbitals
Outer supraorbital
Cavity of cerebral lobes
Rectus oc. int.
Ventricle III
Optic lobes
Periotic cartilage
Ventricle IV
Parts of labyrinth
Medulla
Parachordals
The two notochords
Mesial muscular mass
Outer series of muscle segments
Composite spinal cord


Inner olfactory organs
Olfactory cartilage
United inner eyes and lens
An outer eye
Rectus oc. sup.
Rectus oc. ext.
The two infundibula and their outgrowths
Hyomandibular
Upper parts of gill arches
The two notochords and their parachordals
Oesophagus
Beginning of the two air ducts
Head-kidney
The two notochords
The composite spinal cord


Inner olfactory organs
Olfactory cartilage
Obliquus oc. inf.
Rectus oc. sup.
Optic nerve
Rectus oc. ext.
The two infundibula and their outgrowths
Hyomandibular
The two notochords and their parachordals
Upper parts of gill arches
Beginning of body cavity
Beginning of stomach
Part of liver
Lateral muscles
Mesial muscular mass
The two notochords
The composite spinal cord


Rectus oc. ext.
Olfactory cartilage
Olfactory nerve and pit
Rectus oc. internus
Palato-pterygoid
Rectus oc. int.
Trabeculae cranii
Inward dip of surface epithelium
Anterior ends of united inner Meckel's bars

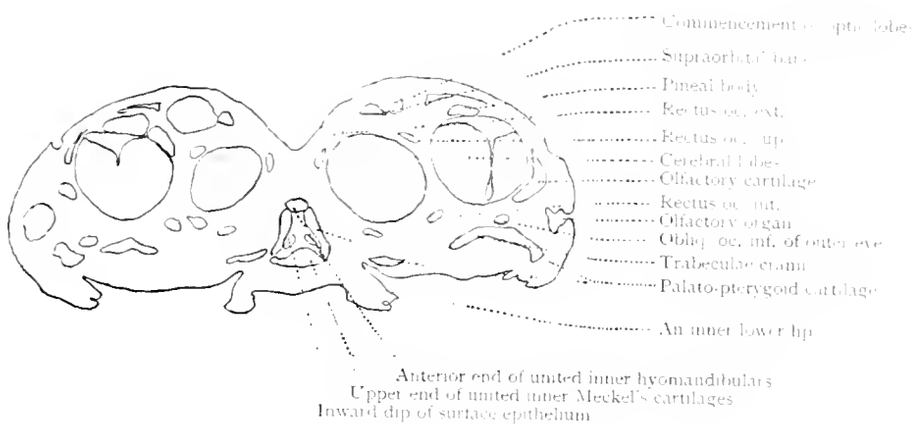

Supraorbital bars
Pineal body
Rectus oc. ext.
Cerebral lobes
Olfactory cartilage
Rectus oc. int.
Olfactory organ
Trabeculae cranii
Palato-pterygoid cartilage
An inner lower lip
Anterior end of united inner hyomandibulars
Upper end of united inner Meckel's cartilages
Inward dip of surface epithelium

FIG. 47.—Transverse section through anterior part of head of double monster belonging to Class II., *i.e.* the type illustrated in Pl. I. fig. 6 (union at medulla). Compare with the series begun in Pl. VIII. fig. 35 (union at optic lobes). The two adjacent eyes are cut through in their posterior halves, near the places of entrance of the optic nerves. The anterior ends of the cerebral lobes belonging to both heads are seen in oblique section, as are also various skeletal elements and ocular muscles. For plane of section see Pl. XXI. figs. 91-93, line 47. Other references are given under Pl. I. fig. 6. (× 18.)

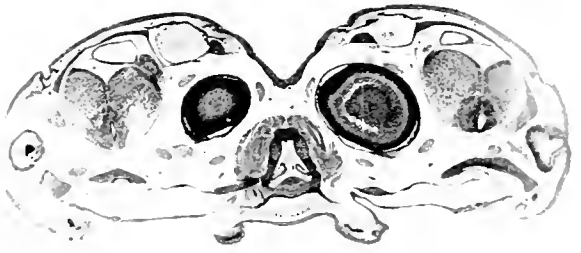


FIG. 48.—Transverse section from same series as last figure, but a short distance further back. Compare with Pl. III. fig. 13 (normal). The section passes through the posterior portions of the adjacent eyes, and through the extreme anterior part of the composite otocyst which represents the fused adjacent auditory organs of the twin heads. The outer eyes lie some distance behind the plane of the section, which is indicated by line 48 in Pl. XXI. figs. 91-93. Other references are given under Pl. I. fig. 6. (× 18.)

FIG. 49.—Transverse section from the same series as Figs. 47, 48, but through the outer eyes, the optic lobes, and the hyomandibular suspensorium on the inner or adjacent sides of the twin heads. Below, in the middle line, is the septum between the two mouth-openings, and in it the inner or adjacent Meckel's cartilages. The moulding of the adjacent united periotic capsules and of the otocysts is extremely interesting. See also the two following figures. Other references are given under Pl. I. fig. 6, and the plane of section is indicated by line 49 in Pl. XXI. figs. 91-93. (×18.)

FIG. 50. Transverse section from the same series as the last three figures, but through the posterior part of the optic lobes, the commencement of the *iter*, the inner hypoaria, the entrance of the optic nerve on one side, and the back part of the mesial oral septum containing the united adjacent hyoids. Other references under Pl. I. fig. 6. (×18.)

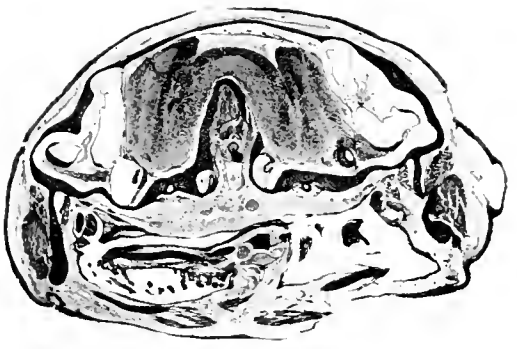
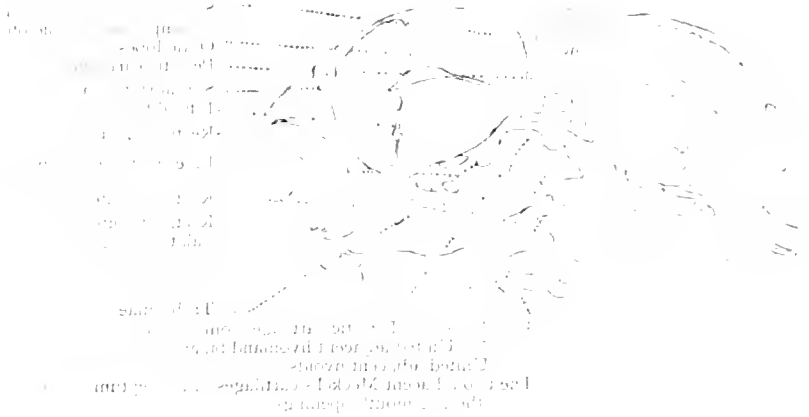
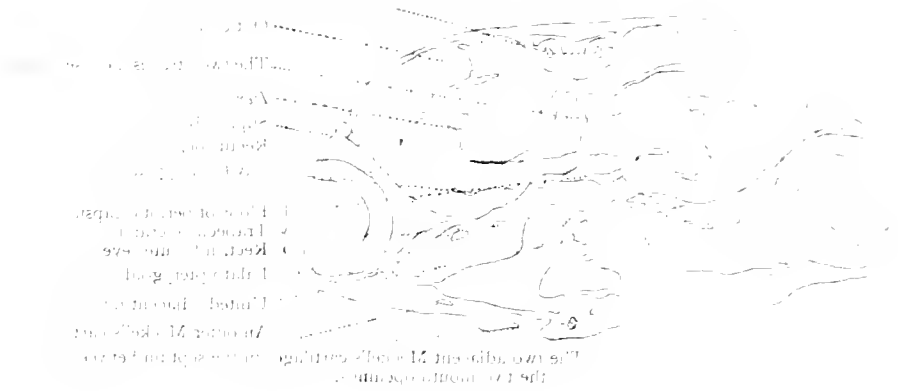
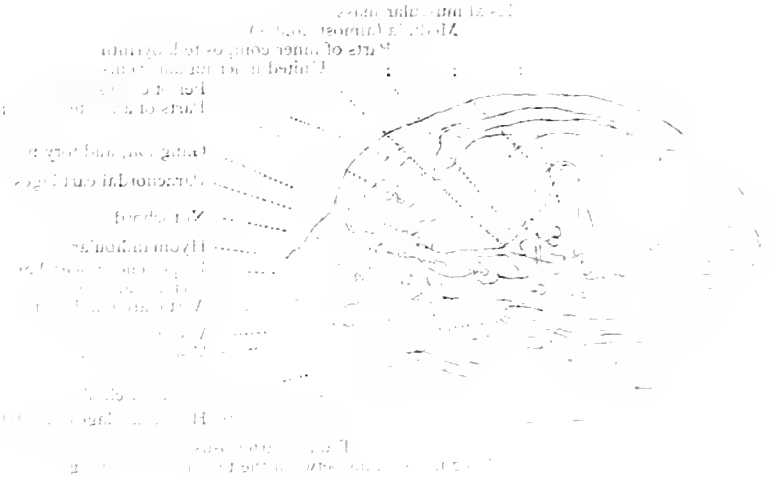
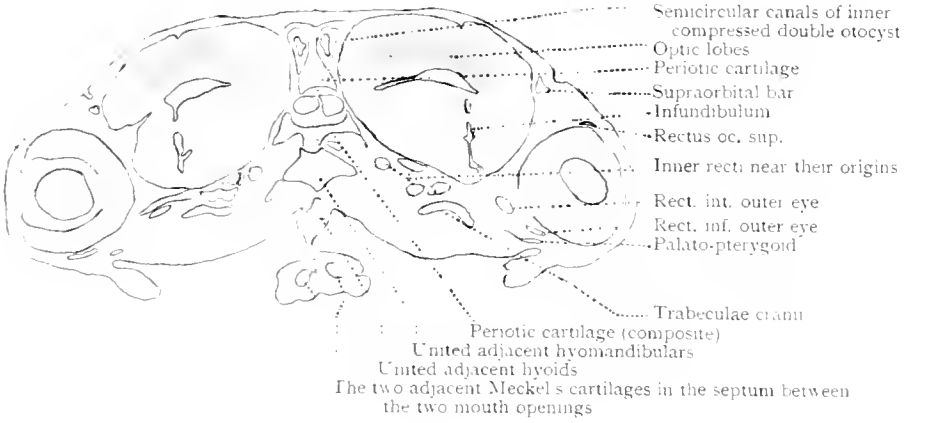


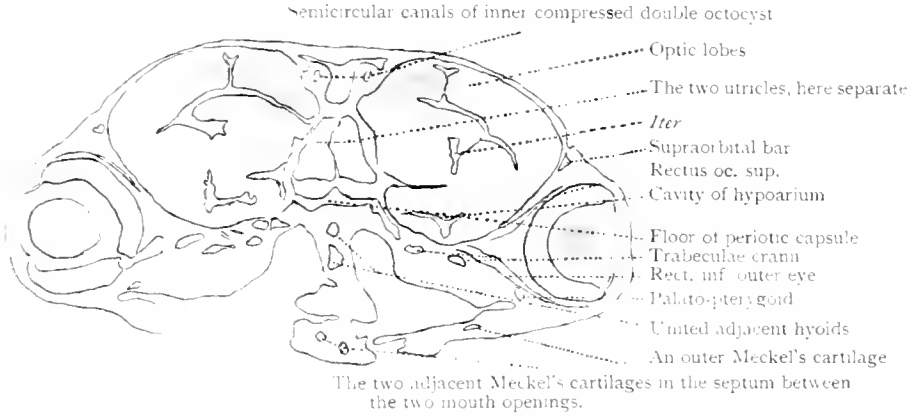
FIG. 51.—Transverse section from same series as the last four figures, but through the outer auditory organs and the posterior part of the brain, which is obviously made up of two converging medullae. The notochord is double, and the inner parachordals have a small mesial mass of muscle wedged in between them. Compare this section with Pl. IV. fig. 18 (normal), and with Pl. IX. fig. 38 (union at optic lobes). Other references under Pl. I. fig. 6, and plane of section in Pl. XXI. figs. 91-93, line 51. (×18.)

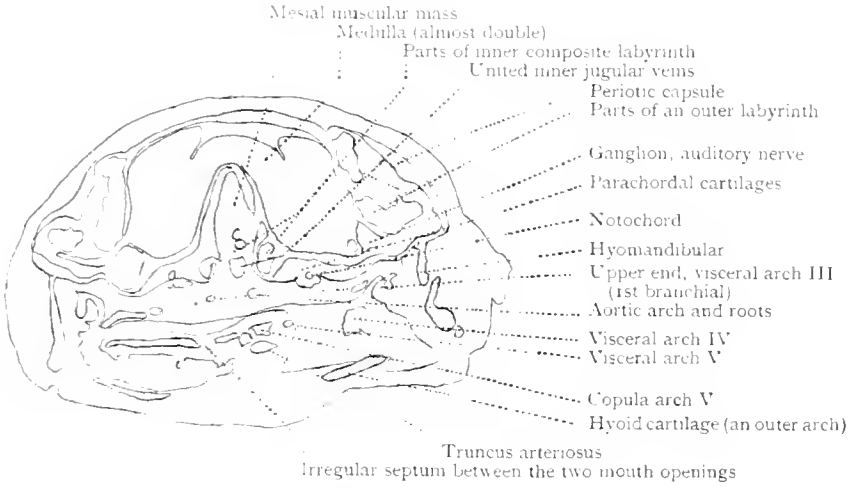


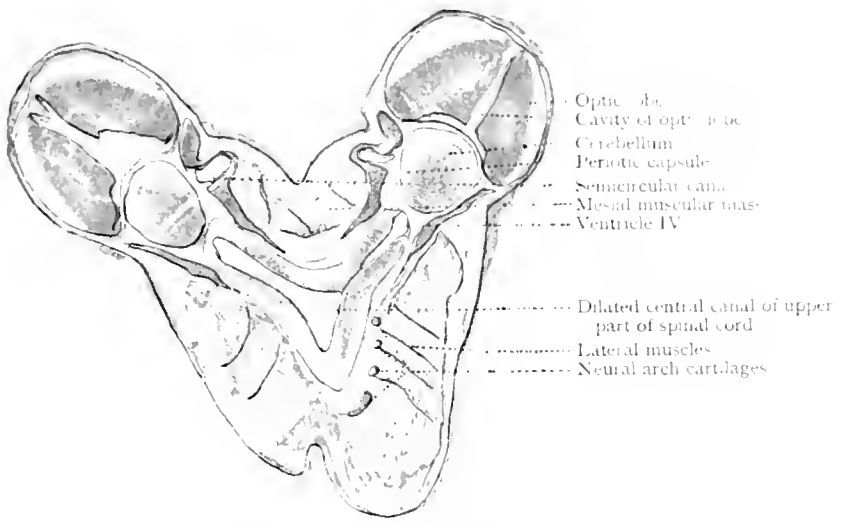


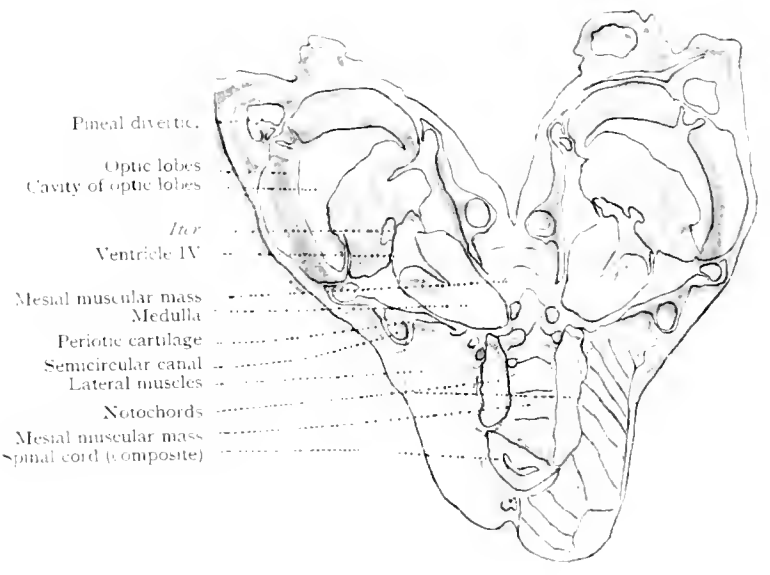


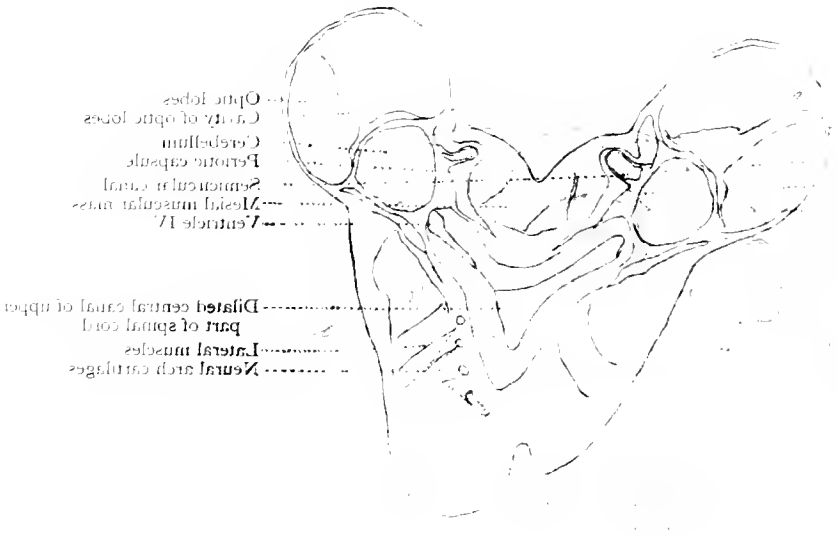

Semicircular canals of inner compressed double otocyst
Optic lobes
Periotic cartilage
Supraorbital bar
Infundibulum
Rectus oc. sup.
Inner recti near their origins
Rect. int. outer eye
Rect. inf. outer eye
Palato-pterygoid
Trabeculae cranii
Periotic cartilage (composite)
United adjacent hyomandibulars
United adjacent hyoids
The two adjacent Meckel's cartilages in the septum between the two mouth openings

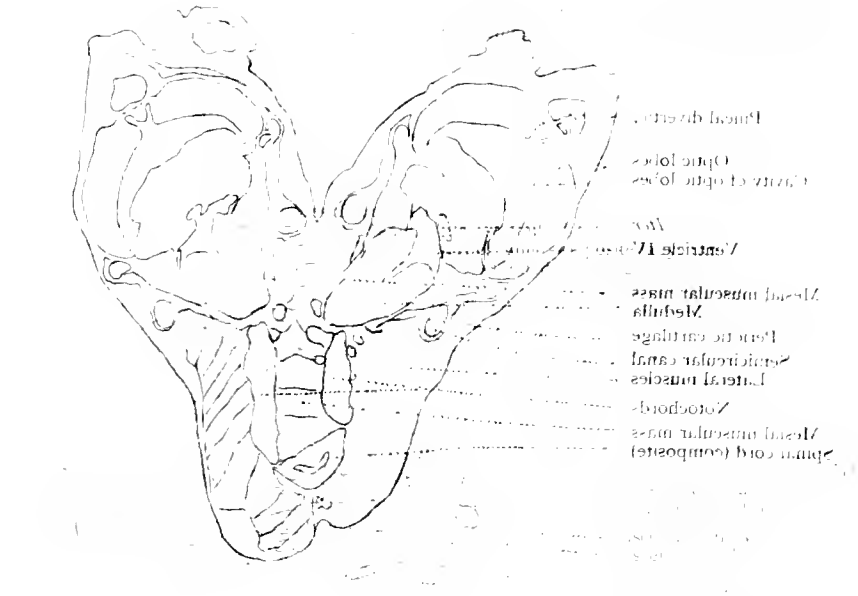

Semicircular canals of inner compressed double octocyst
Optic lobes
The two utricles, here separate
Iter
Supraorbital bar
Rectus oc. sup.
Cavity of hypoarium
Floor of periotic capsule
Trabeculae cranii
Rect. inf. outer eye
Palato-pterygoid
United adjacent hyoids
An outer Meckel's cartilage
The two adjacent Meckel's cartilages in the septum between the two mouth openings.


Mesial muscular mass
Medulla (almost double)
Parts of inner composite labyrinth
United inner jugular veins
Periotic capsule
Parts of an outer labyrinth
Ganglion, auditory nerve
Parachordal cartilages
Notochord
Hyomandibular
Upper end, visceral arch III (1st branchial)
Aortic arch and roots
Visceral arch IV
Visceral arch V
Copula arch V
Hyoid cartilage (an outer arch)
Truncus arteriosus
Irregular septum between the two mouth openings


Optic lobe
Cavity of optic lobe
Cerebellum
Periotic capsule
Semicircular canal
Mesial muscular mass
Ventricle IV
Dilated central canal of upper part of spinal cord
Lateral muscles
Neural arch cartilages


Pineal diverticle
Optic lobes
Cavity of optic lobes
Iter
Ventricle IV
Mesial muscular mass
Medulla
Periotic cartilage
Semicircular canal
Lateral muscles
Notochords
Mesial muscular mass
Spinal cord (composite)


Optic lobes
Cavity of optic lobes
Cerebellum
Petrous capsule
Semicircular canal
Dilated central canal of upper part of spinal cord
Lateral muscles
Neural arch cartilages


Pineal diverticulum
Optic lobes
Cavity of optic lobes
Vertebra IV
Ventricle IV
Dilated central canal of upper part of spinal cord
Lateral muscles
Neural arch cartilages

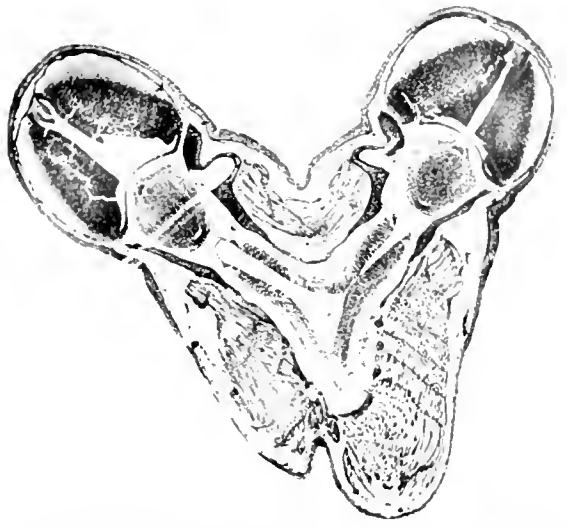


FIG. 52. Horizontal section of double trout monstrosity belonging to the type illustrated in Pl. II. figs. 7, 8 (union in pectoral region). Adjacent pectoral fins are not present. The section passes through the optic lobe masses, the cerebellum, and the upper parts of the periotic cartilages in either head, while, further back, the spinal cord is seen to have its central cavity much dilated and bifurcating into the two fourth ventricles. Compare with Pl. V. fig. 21 (normal), and with Pl. X. fig. 39 and Pl. XII. fig. 43 (union at optic lobes). For other references see under Pl. II. fig. 7. (× 20.)

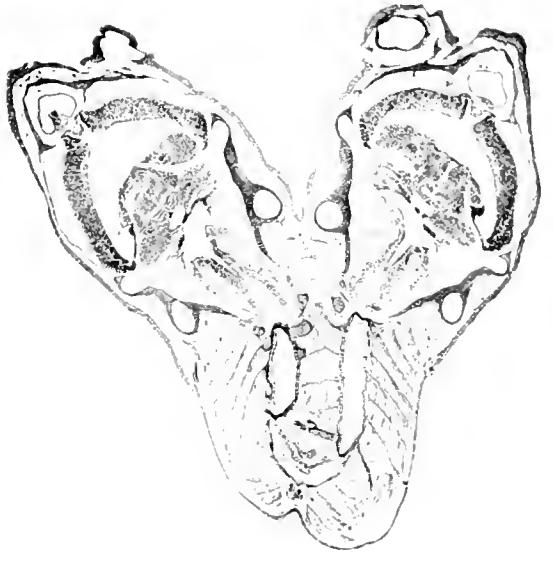


FIG. 53. Horizontal section belonging to the same series as Fig. 52, but at a slightly deeper level. The section passes through the cavities of the pineal bodies, of the optic lobes, the *Iter*, and fourth ventricle. As in Pls. X.–XII. figs. 39-46, owing to the curvature of the specimen, the trunk is cut through obliquely. The section here shows the composite spinal cord, the two outer series of muscle segments, and a mesial similar series between the two notochords. For other references see under Pl. II. fig. 7. (× 20.)

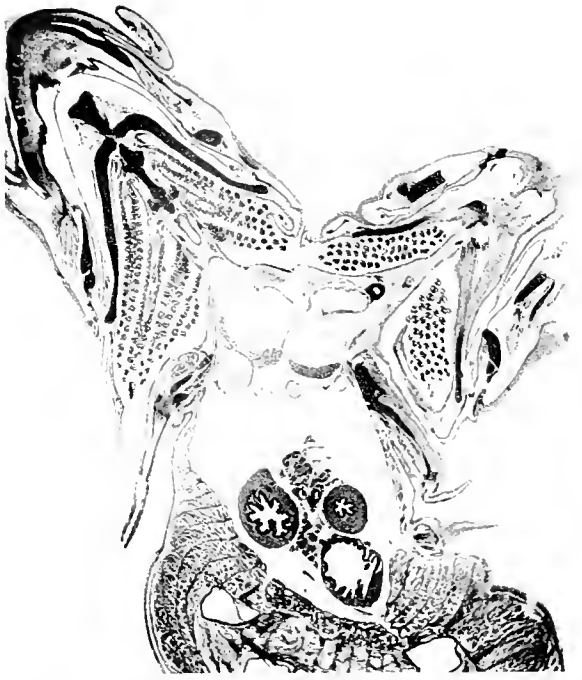


FIG. 54.—Horizontal section belonging to the same series as the last, but at a distinctly deeper level. Some of the gill-arch structures are seen in either head in front, and behind these certain chambers of the double heart, which lies inside a single large pericardial cavity. The alimentary canals are double down to the level of the stomach. Two bile ducts enter the first part of the composite intestine. For references see under Pl. II. fig. 7. (×20)

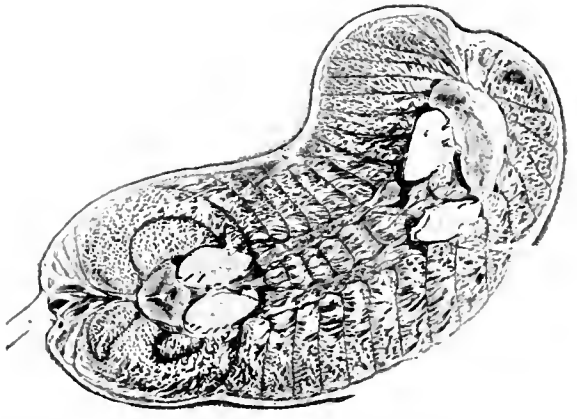
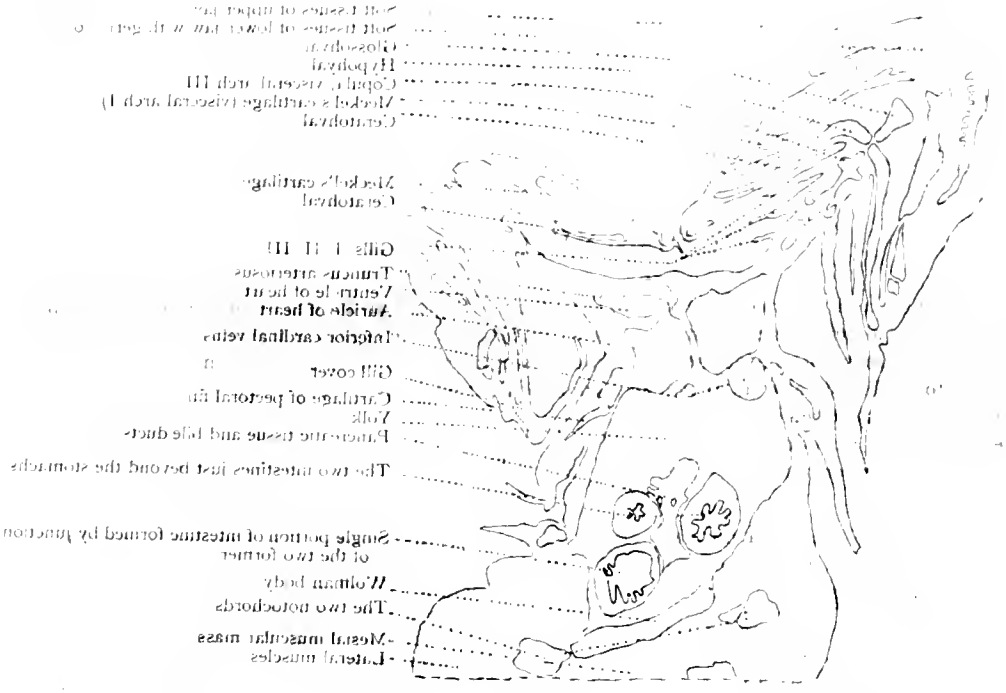
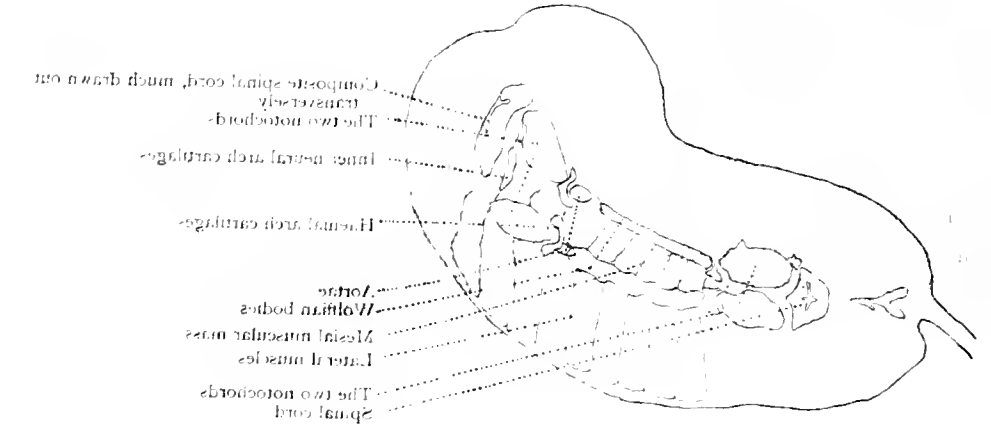
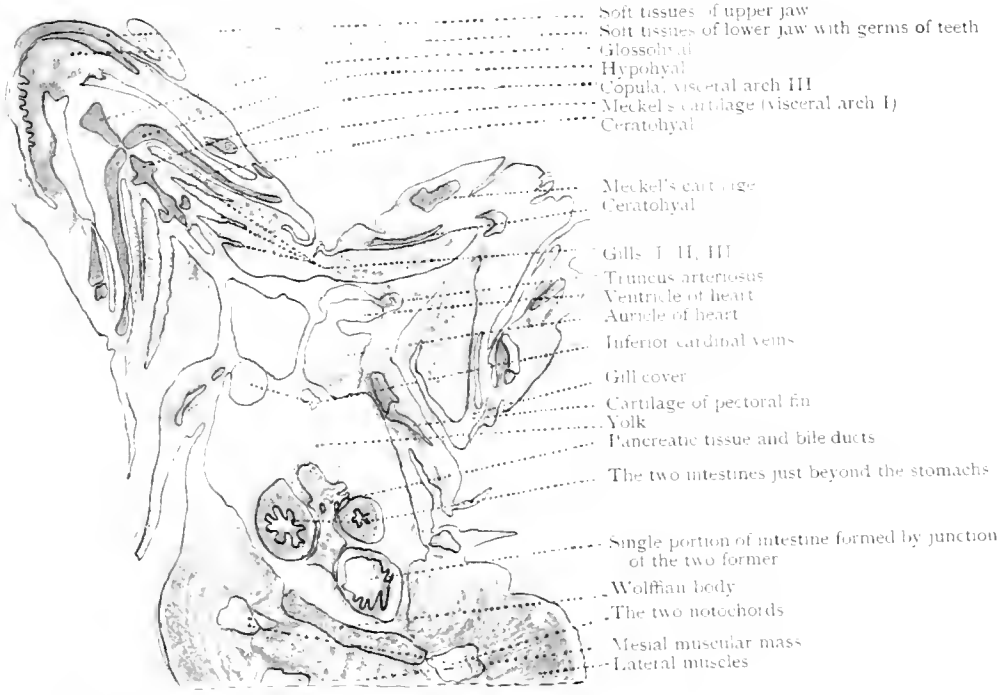


FIG. 55.—Horizontal section further back in the same series as the last. The section passes through the sharply curved portion of the body behind the place of union. The spinal cord is cut in two places; its proximal section is drawn out transversely and is obviously composite, while the distal section is almost normal. Both regions have a pair of notochords. The mesial muscular mass between the notochords is well illustrated here, and is seen to be divided into a series of segments corresponding with the two outer series of muscular segments. The disposition of the adjacent neural arch cartilages is also indicated. References under Pl. II. fig. 7. (×28.)






Soft tissues of upper jaw
Soft tissues of lower jaw with germs of teeth
Glossohyal
Hypohyal
Copula, visceral arch III
Meckel's cartilage (visceral arch I)
Ceratohyal
Meckel's cartilage
Ceratohyal
Gills I, II, III
Truncus arteriosus
Ventricle of heart
Auricle of heart
Inferior cardinal veins
Gill cover
Cartilage of pectoral fin
Yolk
Pancreatic tissue and bile ducts
The two intestines just beyond the stomachs
Single portion of intestine formed by junction of the two former
Wolffian body
The two notochords
Mesial muscular mass
Lateral muscles

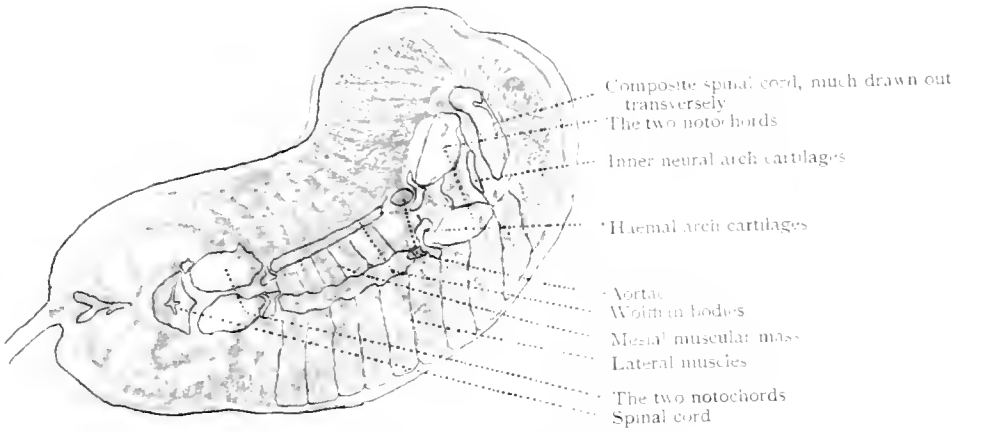

Composite spinal cord, much drawn out transversely
The two notochords
Inner neural arch cartilages
Haemal arch cartilages
Aortae
Wolffian bodies
Mesial muscular mass
Lateral muscles
The two notochords
Spinal cord

PLATE XVII

FIG. 56.—Diagram of cranial and hyomandibular skeleton of a normal trout embryo, about six weeks after hatching, and of same age as the monstrosities examined. The structures are supposed to be looked at from above after removal of the roof cartilages by a section passing horizontally through the nasal and periotic cartilages. For description see p. 11, and for other references see under Pl. I. fig. 1.

FIG. 57.—The roof cartilages of the skull of a normal trout embryo, looked at from above. References to description and illustrations as under Fig. 56.

FIG. 58.—Diagram of cranial and hyomandibular skeleton of a double monster embryo, of the type (Class I.) illustrated in Pl. I. figs. 4, 5, &c. with union of the twin brains at the optic lobes. As in Fig. 56, the structures are supposed to be looked at from above after removal of the roof cartilages by a section passing horizontally through the nasal and periotic cartilages. The duplicity affects anterior structures only. See also Fig. 59. Description on p. 13, and other references under Pl. I. fig. 4.

FIG. 59.—Diagram showing the roof cartilages of the double monster illustrated in the preceding figure.

FIG. 60.—Diagram illustrating the cranial and hyomandibular skeleton in a double monster belonging to Class II., &c. with union of the *twin* brains at the medulla oblongata. The view is from above after removal of the roof cartilages as in Figs. 56, 58. For description see p. 16, and for other references Pl. I. fig. 6.

FIG. 61.—Diagram showing from above the roof cartilages of the skull of the double monster illustrated in Fig. 60. For general references see under Fig. 60.

FIG. 62.—Diagram of neural and basonal arch cartilages in a normal trout embryo, six weeks after hatching. See p. 12.

FIG. 63.—Typical arrangement of neural and basonal arch cartilages at the region of transition from the double to the single condition, in a double monster exhibiting union of the twin bodies. See p. 13.

EXPLANATION TO PL. XVII. FIGS. 56–63.

a. Olfactory capsular cartilage.
b. Trabeculae cranii.
bb. Hypobranchial cartilage. (The glossohyal is omitted — see Pl. XVIII. fig. 64.)
c. Parachordal cartilages.
d. Is placed on the trabeculae cranii just in front of the pituitary space in Fig. 56, or the two pituitary spaces in Figs. 58, 60.
e. Is placed on the parachordals just behind the pituitary space in Fig. 56, or the two pituitary spaces in Figs. 58, 60.
f. Palato-pterygoid bar (*f'*, inner or adjacent pterygoid bar).
g, g, g. Anterior, middle, and posterior fontanelles.
g'. Meckel's cartilage of lower jaw (*g'* inner or adjacent Meckel's cartilage of lower jaw).
h. Hyoid bar.
hh. Hæmal arch cartilage (*hh'* inner or adjacent hæmal arch cartilage).
i. Hyomandibular (*i'*, inner or adjacent hyomandibular).
k. On floor of periotic capsule (*k'*, on floor of inner or adjacent periotic capsule).
m. Pituitary space with external rectus muscles passing through it.
Na. Neural arch cartilage (*Na'*, inner or adjacent neural arch cartilage).
Nch. Notochord.
o. Roof part of olfactory capsular cartilage.
s. Suprabasal bars (*s'*, inner or adjacent suprabasal bars).
sp. Spinal cord.
t. Cartilage of roof of periotic capsule.
tr. Lamina part of parachordals.
Ne. Terminal cartilages above the third ventricle and cerebellum respectively.

PLATE XVII

FIG. 56.—Diagram of cranial and hyomandibular skeleton of a normal trout embryo, about six weeks after hatching, and of same age as the monstrosities examined. The structures are supposed to be looked at from above after removal of the roof cartilages by a section passing horizontally through the nasal and periotic cartilages. For description see p. 11, and for other references see under Pl. I. fig. 1.

FIG. 57.—The roof cartilages of the skull of a normal trout embryo, looked at from above. References to description and illustrations as under Fig. 56.

FIG. 58.—Diagram of cranial and hyomandibular skeleton of a double monster embryo, of the type (Class I.) illustrated in Pl. I. figs. 4, 5, *i.e.* with union of the twin brains at the optic lobes. As in Fig. 56, the structures are supposed to be looked at from above after removal of the roof cartilages by a section passing horizontally through the nasal and periotic cartilages. The duplicity affects anterior structures only. See also Fig. 59. Description on p. 13, and other references under Pl. I. fig. 4.

FIG. 59.—Diagram showing the roof cartilages of the double monster illustrated in the preceding figure.

FIG. 60.—Diagram illustrating the cranial and hyomandibular skeleton in a double monster belonging to Class II., *i.e.* with union of the twin brains at the medulla oblongata. The view is from above after removal of the roof cartilages as in Figs. 56, 58. For description see p. 16, and for other references Pl. I. fig. 6.

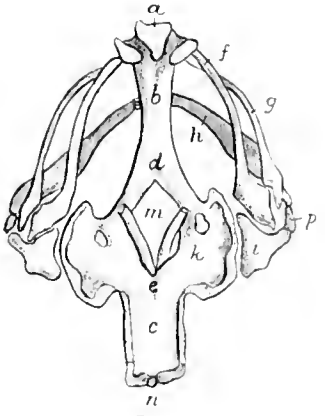
FIG. 61.—Diagram showing from above the roof cartilages of the skull of the double monster illustrated in Fig. 60. For general references see under Fig. 60.

FIG. 62.—Diagram of neural and haemal arch cartilages in a normal trout embryo, six weeks after hatching. See p. 12.

FIG. 63.—Typical arrangement of neural and haemal arch cartilages at the region of transition from the double to the single condition, in a double monster exhibiting union of the twin bodies. See p. 13.

LETTERING IN PL. XVII. FIGS. 56-63.

a. Olfactory capsular cartilage.
b. Trabeculae cranii.
bh. Hypohyal cartilage. (The glossohyal is omitted; see Pl. XVIII fig. 64.)
c. Parachordal cartilages.
d. Is placed on the trabeculae cranii just in front of the pituitary space in Fig. 56, or the two pituitary spaces in Figs. 58, 60.
e. Is placed on the parachordals just behind the pituitary space in Fig. 56, or the two pituitary spaces in Figs. 58, 60.
f. Palato-pterygoid bar (*f'*, inner or adjacent palato-pterygoid bar).
f_1, f_2, f_3. Anterior, middle, and posterior fontanelles.
g. Meckel's cartilage of lower jaw (*g'* inner or adjacent Meckel's cartilage of lower jaw).
h. Hyoid bar.
ha. Haemal arch cartilage (*ha'* inner or adjacent haemal arch cartilage).
i. Hyomandibular (*i'*, inner or adjacent hyomandibular).
k. On floor of periotic capsule (*k'*, on floor of inner or adjacent periotic capsule).
m. Pituitary space with external recti muscles passing through it.
Na. Neural arch cartilage (*Na'*, inner or adjacent neural arch cartilage).
Nch. Notochord.
r. Roof part of olfactory capsular cartilage.
s. Supraorbital bars (*s'*, inner or adjacent supraorbital bars).
spc. Spinal cord.
t. Cartilage of roof of periotic capsule.
w. Laminar part of parachordals.
xy. Tegminal cartilages above the third ventricle and cerebellum respectively.



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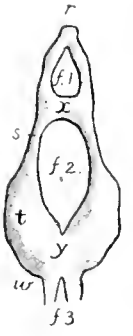

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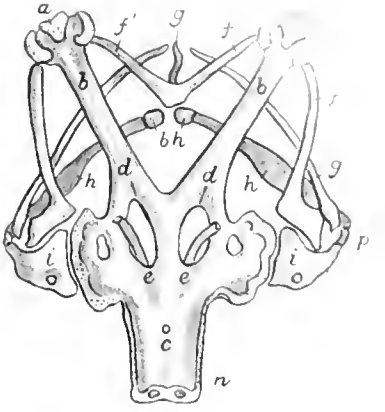

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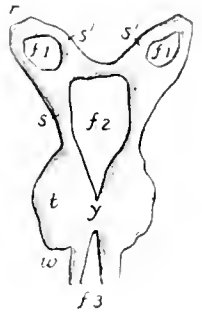

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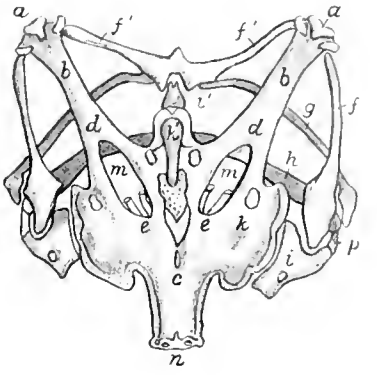

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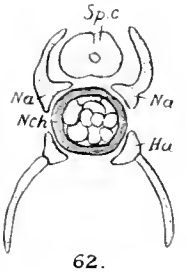

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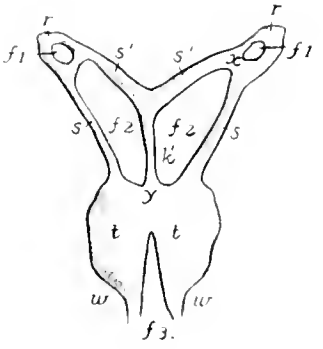

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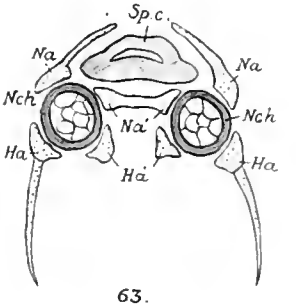

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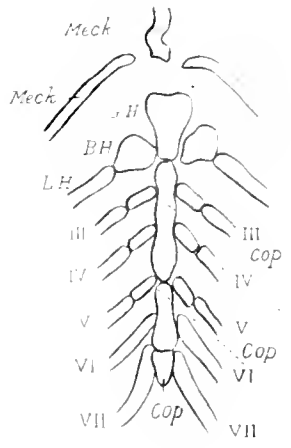

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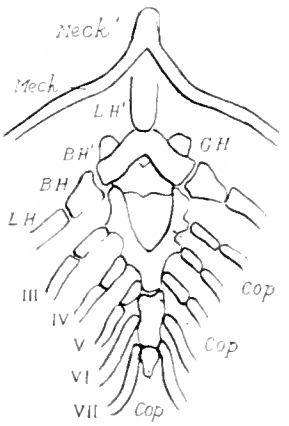

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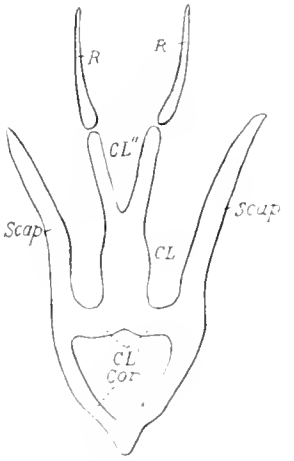

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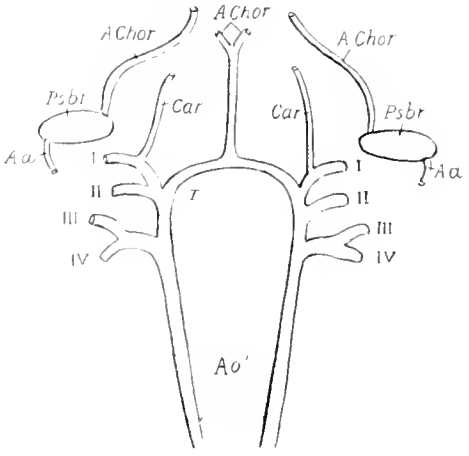

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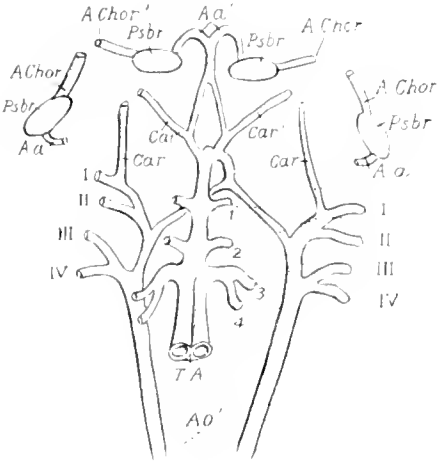

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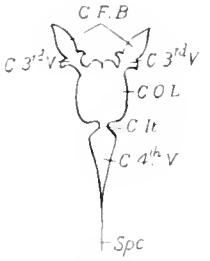

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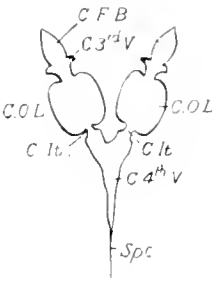

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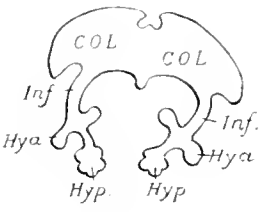


72.

PLATE XVIII

FIG. 64.—Ventral ends of the Meckelian, hyoid, and succeeding visceral arch cartilages of a double monster belonging to Class I. For general references see under Pl. I. fig. 4. Lettering as in the succeeding figure.

FIG. 65.—Ventral ends of the Meckelian, hyoid, and succeeding visceral arch cartilages of a double monster belonging to Class II. For general references see under Pl. II. fig. 6.

Meck. Outer Meckelian bars.
Meck'. Inner or adjacent Meckelian bars united and greatly reduced.
GH. Glossohyal.
BH. Hypohyal.
LH. Ceratohyal.
BH'. Inner or adjacent hypohyals partly united.
LH'. ,, ,, ceratohyals united.
III, IV, V, VI, VII. The branchial cartilages.
Cop. Copular pieces, the anterior one being bifid.

FIG. 66.—Transverse section of skeleton of composite pectoral fin from a double monster belonging to Class IV., in which union of the twin bodies took place just behind the pectoral fins. Description on p. 19.

Scap., Cor. Scapular and coracoid parts respectively of the coracoscapular bars. The ventral ends of the coracoids are united.
CL. The limb-cartilages united for the greater part of their length.
R. The rays (not cartilaginous).

FIG. 67.—Diagram illustrating the dorsal aorta and its roots in the double monster belonging to Class I., from which Pl. XVIII. fig. 64 was taken. For references see under Pl. I. fig. 4.

Ao'. Aorta, the two limbs uniting further back.
II, I, III, IV. Aortic roots, *i.e.* branchial veins.
Car. Carotids.
Aa. Artery to pseudobranch, a branch of the hyoid artery.
Psbr. Pseudobranch.
A.Chor. Choroidal artery.
A.Chor'. The arteries for the choroidal glands of the inner or adjacent pair of eyes. They arise by a single stem from the middle of a vessel connecting the aortic roots on either side, and go to the choroidal glands without passing through a pseudobranch.

FIG. 68.—Diagram illustrating the ventral aorta, the dorsal aorta, and the aortic roots in the double monster belonging to Class II., from which Pl. XVII. fig. 60 was taken. For references see under Pl. II. fig. 6. Lettering as in Fig. 67 with additional:

VA. Ventral aorta and its branches 1, 2, 3, 4.
Car'. Inner or adjacent carotids, giving off *Aa'.* arteries to the inner or adjacent pseudobranchs *Psbr'.*

It will be seen that there are two sets of carotid and afferent pseudobranch arteries, the inner sets being derived directly from the ventral aorta. The ventral aorta arches dorsally in the septum between the two mouths of the monstrosity, reaches the base of the skull, and then divides into two limbs which are continued backwards to join the aortic-collecting roots on either side.

FIG. 69.—Outline of central cavity of brain of normal trout embryo. Lettering as in Fig. 71. For references see under Pl. I. fig. 1.

FIG. 70.—Outline of central cavity of brain of the double monster (Class I.) illustrated in Pl. XVII. fig. 58. Lettering as in Fig. 71. For references see under Pl. I. fig. 4.

FIG. 71.—Outline of central cavity of brain in the double monster (Class I.) illustrated in Pl. XVII. fig. 60. For references see under Pl. II. fig. 6.

C.E.B. Cavity of the hemispheres.
C.3rd V. ,, 3rd ventricle.
C.OL. ,, optic lobes.
CH. ,, iter a tertio ad quartum ventriculum.
C.4th V. ,, 4th ventricle.
Sp. ,, spinal cord.

FIG. 72.—Outline of transverse section of central cavity (in anterior part of optic lobe region of the brain illustrated in Fig. 70 (*q.v.*). There are two infundibula and two sets of hypoarial cavities, while the main optic lobe cavity is single.

C.OL. Cavity of optic lobes.
Inf. Infundibulum.
Hyp. Hypophysis sac.
Hya. One of the hypoarial cavities.

PLATE XVIII

FIG. 64.—Ventral ends of the Meckelian, hyoid, and succeeding visceral arch cartilages of a double monster belonging to Class I. For general references see under Pl. I. fig. 4. Lettering as in the succeeding figure.

FIG. 65.—Ventral ends of the Meckelian, hyoid, and succeeding visceral arch cartilages of a double monster belonging to Class II. For general references see under Pl. II. fig. 6.

Meck. Outer Meckelian bars.
Meck'. Inner or adjacent Meckelian bars united and greatly reduced.
GH. Glossohyal.
BH. Hypohyal.
LH. Ceratohyal.
BH'. Inner or adjacent hypohyals partly united.
LH'. ,, ,, ceratohyals united.
III, IV, V, VI, VII. The branchial cartilages.
Cop. Copular pieces, the anterior one being bifid.

FIG. 66.—Transverse section of skeleton of composite pectoral fin from a double monster belonging to Class IV., in which union of the twin bodies took place just behind the pectoral fins. Description on p. 19.

Scap., Cor. Scapular and coracoid parts respectively of the coracoscapular bars. The ventral ends of the coracoids are united.
CL. The limb-cartilages united for the greater part of their length.
R. The rays (not cartilaginous).

FIG. 67.—Diagram illustrating the dorsal aorta and its roots in the double monster belonging to Class I., from which Pl. XVIII. fig. 64 was taken. For references see under Pl. I. fig. 4.

Ao. Aorta, the two limbs uniting further back.
II, I, III, IV. Aortic roots, *i.e.* branchial veins.
Car. Carotids.
Aa. Artery to pseudobranch, a branch of the [illegible] artery.
Psbr. Pseudobranch.
Chor. Choroidal artery.
A.Chor'. The arteries for the choroidal glands of the inner or adjacent pair of eyes. They are [illegible] single stem from the middle of a vessel connecting the aortic roots on either side, and go to the choroidal glands without passing through a pseudobranch.

FIG. 68.—Diagram illustrating the ventral aorta, the dorsal aorta, and the aortic roots in the double monster belonging to Class II., from which Pl. XVII. fig. 60 was taken. For references see under Pl. II. fig. 6. Lettering as in Fig. 67 with additional:

Z.A. Ventral aorta and its branches 1, 2, 3, 4.
Car'. Inner or adjacent carotids, giving off *Aa'.* arteries to the inner or adjacent pseudobranchs *Psbr'.*

It will be seen that there are two sets of carotid and afferent pseudobranch arteries, the inner sets being derived directly from the ventral aorta. The ventral aorta arches dorsally in the septum between the two mouths of the monstrosity, reaches the base of the skull, and then divides into two limbs which are continued backwards to join the aortic-collecting roots on either side.

FIG. 69.—Outline of central cavity of brain of normal trout embryo. Lettering as in Fig. 71. For references see under Pl. I. fig. 1.

FIG. 70.—Outline of central cavity of brain of the double monster (Class I.) illustrated in Pl. XVII. fig. 58. Lettering as in Fig. 71. For references see under Pl. I. fig. 4.

FIG. 71.—Outline of central cavity of brain in the double monster (Class I.) illustrated in Pl. XVII. fig. 60. For references see under Pl. II. fig. 6.

C.H.B. Cavity of the hemispheres.
C.3rd V. ,, 3rd ventricle.
C.O.L. ,, optic lobes.
C.V. ,, inter a tertio ad quartum ventriculum.
C.4th V. ,, 4th ventricle.
Spc. ,, spinal cord.

FIG. 72.—Outline of transverse section of central cavity (an anterior part of optic lobe region) of the brain illustrated in Fig. 70 (*q.v.*). There are two infundibula and two sets of hypoarial cavities, while the main optic lobe cavity is single.

O.L. Cavity of optic lobes.
Inf. Infundibulum.
Hyp. Hypophysis [illegible].
Hyc. One of the hypoarial cavities.

PLATE XIX

PLATE XIX

FIG. 73.—Diagram of heart, etc., of normal trout embryo (p. 12). Lettering as in Fig. 75. Above s.v. is the common opening of the anterior jugular veins. For general references see under Pl. I. fig. 1.

FIG. 74.—Diagram of the heart, etc., of the double monster (Class III.) illustrated in Pl. II. fig. 7, which see for general references. Lettering as in Fig. 75.

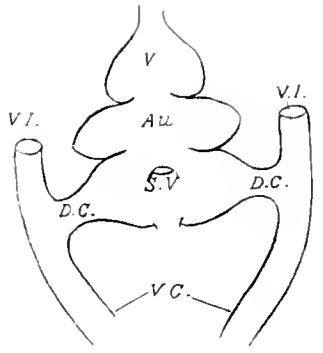
FIG. 75.—Diagram of the heart, etc., of a double monster belonging to Class IV., *i.e.* with union in pectoral region, the adjacent pectoral fins being present but united (p. 19).

V. Ventricle.
Au. Auricle.
SV. Sinus venosus.
DC. Duct of Cuvier.
DC'. Inner or adjacent ducts of Cuvier.
VJ. Jugular vein.
VC. Cardinal vein (posterior).
VC'. Inner or adjacent cardinal veins.

FIG. 76.—Diagram illustrating the Wolffian duct and urinary bladder in a normal trout embryo (p. 12). Lettering as in Figs. 77-81. For references see under Pl. I. fig. 1.

FIGS. 77–81.—Diagrams illustrating the arrangement of the Wolffian ducts and bladders according to the different types described on pp. 21-23. It will be noted that the ducts which associate themselves in pairs with the bladders nearly always consist of the right duct of one embryo and the left of the other. Fig. 80 is an exception, and Fig. 81 an example of pure ventral union (p. 23).

BL. Bladder.
BL'. Bladder formed by the inner or adjacent pair of Wolffian ducts.
WD. Wolffian ducts.
WDb, *WDb'*. Wolffian ducts belonging to one of the twins in each of the figures.
WDc, *WDc'*. Wolffian ducts belonging to the other twin in each of the figures.
Int. Intestine.
R. Rectum.
V. Vent.
P. Urinary pore.



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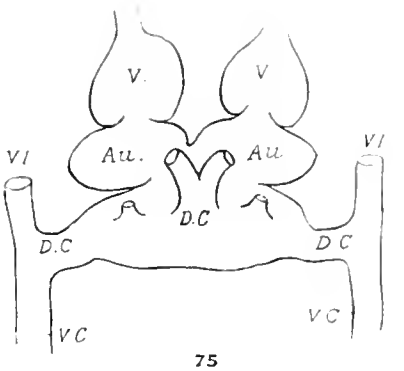

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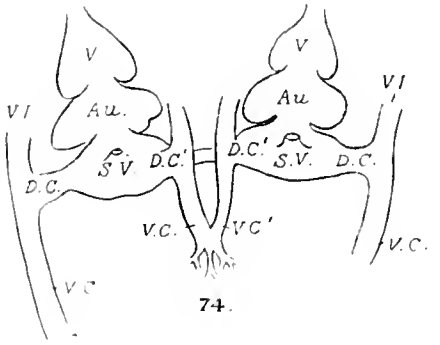

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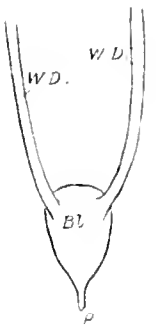

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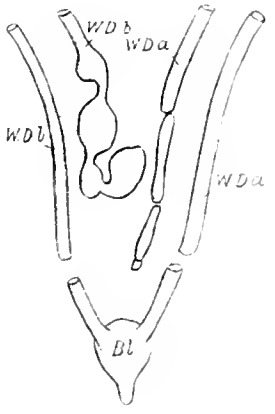

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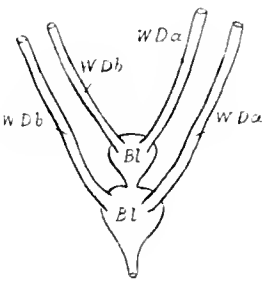

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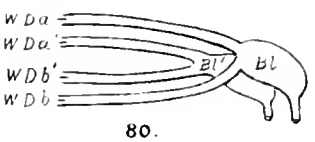

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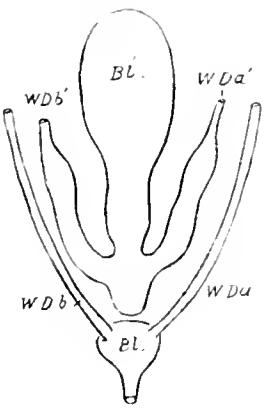

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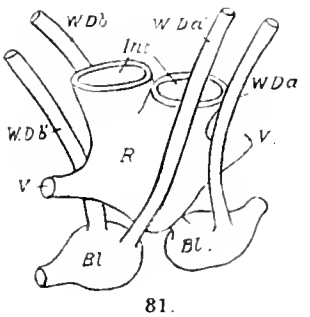

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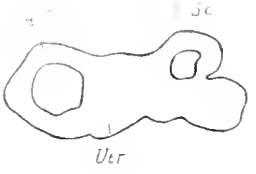

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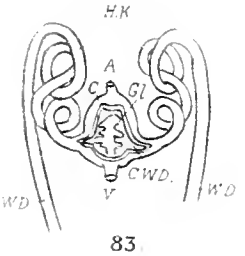

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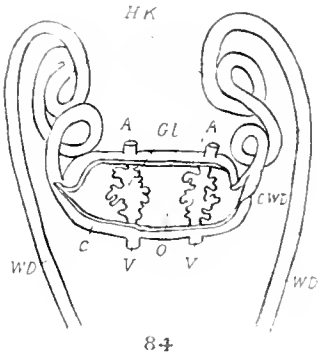

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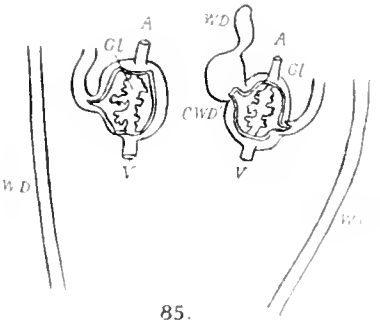

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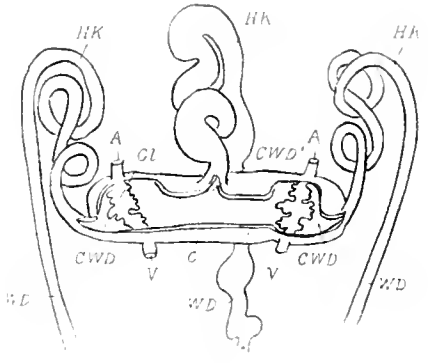

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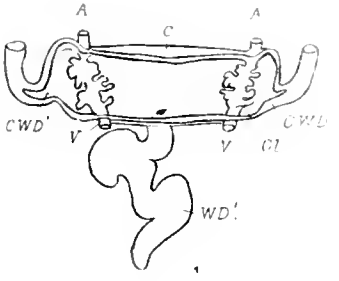


87.

PLATE XX

FIG. 82.—Lateral view of the composite auditory sac present in the angle between the twin heads of a double monster belonging to Class II., *i.e.* with union of the twin brains at the medulla oblongata. Description on p. 17, and other references under Pl. I. fig. 6.

Utr. Utricle.
a. c. An anteriorly placed semicircular canal.
p. c. A posteriorly " "

FIG. 83.—Diagram of head-kidney of a normal trout embryo (p. 12).

GL. Glomerular tuft of vessels.
A. Afferent vessel.
E. Efferent vessel.
c Capsule of glomerulus.
c.WD. Commencement of Wolffian duct *WD*.
HK. Cells of Wolffian duct in head-kidney.

FIG. 84.—Composite head-kidney in a double monstrosity, of the type described on p. 14. Lettering as in Fig. 83. Two glomerular tufts are present in a cavity divided into three chambers.

O. Mesial chamber.

FIG. 85.—Head-kidney in a double monstrosity of same general type as last, but here the glomeruli have not united together, though the adjacent halves of each give origin to no Wolffian ducts or only to a short blind one. Lettering as in Fig. 82.

FIGS. 86 AND 87.—Head-kidney glomeruli of other two double monstrosities showing a degree of duplicity greater than that illustrated in Fig. 85. A blind sacculated tube comes off from the middle compartment of the composite glomerulus and represents united adjacent Wolffian ducts.

PLATE XX

FIG. 82.—Lateral view of the composite auditory sac present in the angle between the twin heads of a double monster belonging to Class II., *i.e.* with union of the twin brains at the medulla oblongata. Description on p. 17, and other references under Pl. I. fig. 6.

A. Utricle.
B. An anteriorly placed semicircular canal.
C. A posteriorly [illegible]

FIG. 83.—Diagram of head-kidney of a normal trout embryo (p. 12).

GA. Glomerular tuft of vessels.
A. Afferent vessel.
E. Efferent vessel.
C. Capsule of glomerulus.
HZ. Commencement of Wolffian duct HZ.
WA. Coils of Wolffian duct in head kidney.

FIG. 84.—Composite head-kidney in a double monstrosity, of the type described on p. 14. Lettering as in Fig. 83. Two glomerular tufts are present in a cavity divided into three chambers.

G. Mesial chamber.

FIG. 85.—Head-kidney in a double monstrosity of same general type as last, but here the glomeruli have not united together, though the adjacent halves of each give origin to no Wolffian ducts or only to a short blind one. Lettering as in Fig. 82.

FIGS. 86 AND 87.—Head-kidney glomeruli of other two double monstrosities showing a degree of duplicity greater than that illustrated in Fig. 85. A blind sacculated tube comes off from the middle compartment of the composite glomerulus and represents united adjacent Wolffian ducts.

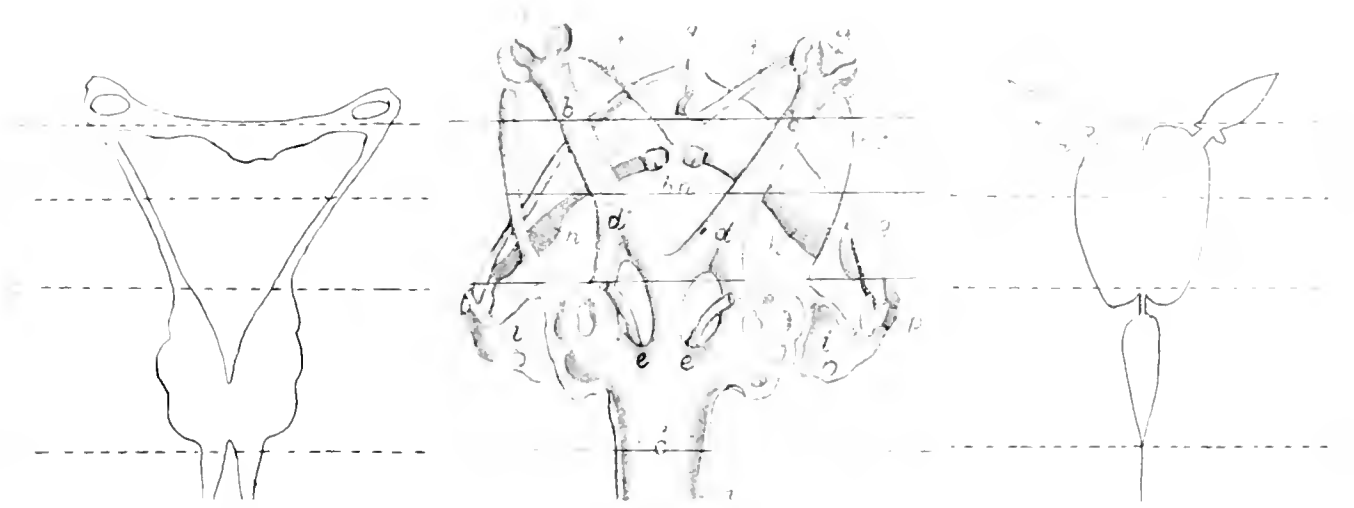


FIG. 87. FIG. 88. FIG. 89.

FIGS. 88, 89.—Reconstruction diagrams of the cranial cartilaginous skeleton in a double monster belonging to Class I., *a*, with union in the region of the optic lobes. Fig. 88 is a view from above of the skeletal parts after removal of the roof cartilages by a section passing horizontally through the olfactory and the auditory capsular cartilages. Fig. 88 also includes the mandibular and hyoid arches, which for diagrammatic purposes are represented as wider than normal. The transverse lines numbered 35, 36, 37, 38, indicate respectively the planes and levels of the various transverse sections shown in Pls. VIII., IX., figs. 35, 36, 37, 38. Fig. 89 represents the roof parts of the skull with transverse lines having the same meaning as in Fig. 88 (see explanation under Pl. XVII. fig. 50). The general references to Class I. will be found under Pl. I. fig. 4. (× approx. 15.)

FIG. 90.—Diagrammatic outline of the central cavities of the brain in the same double monster as that from which Figs. 88 and 89 were taken. The transverse lines have the same meaning as in these figures. The large composite cavity of the mid-brain (optic lobes) is seen to lead, in front, into the cavities of the two forebrains, and, behind, into that of the single medulla (see under Pl. XVIII. fig. 70).

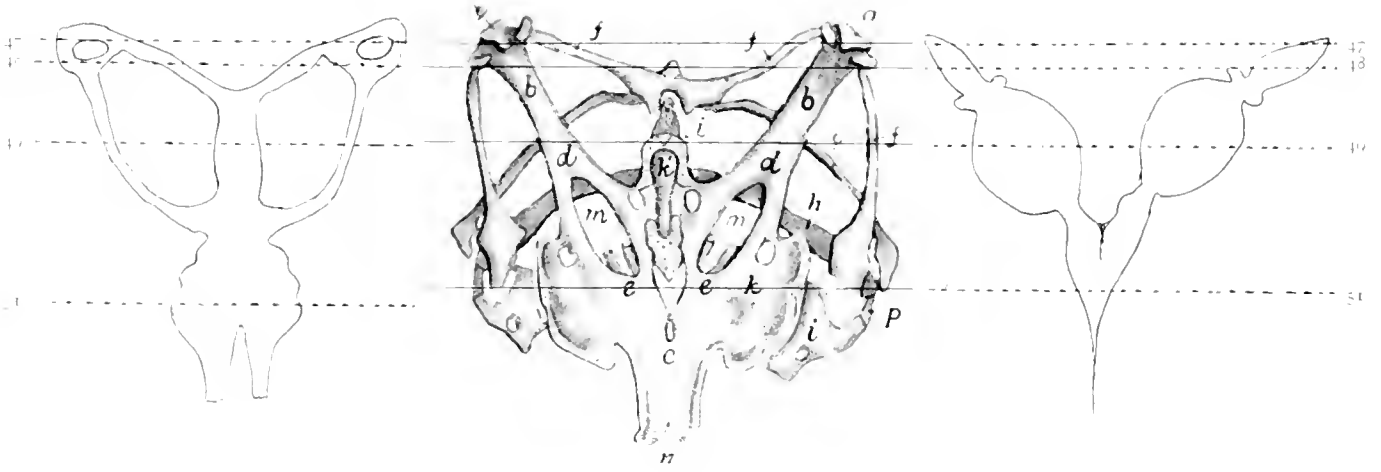


FIG. 92. FIG. 91. FIG. 93.

FIGS. 91-93.—Diagrams of the cartilaginous cranial skeleton and of the brain cavities in a double monster belonging to Class II., *a*, with union in the region of the medulla. The numbered transverse lines are for the same purpose, and have the same meaning as in Pl. XXI. figs. 88-90. The general references to Class II. are given under Pl. I. fig. 6. See also under Pl. XVII. fig. 61, XVIII. fig. 71. (× approx. 15.)

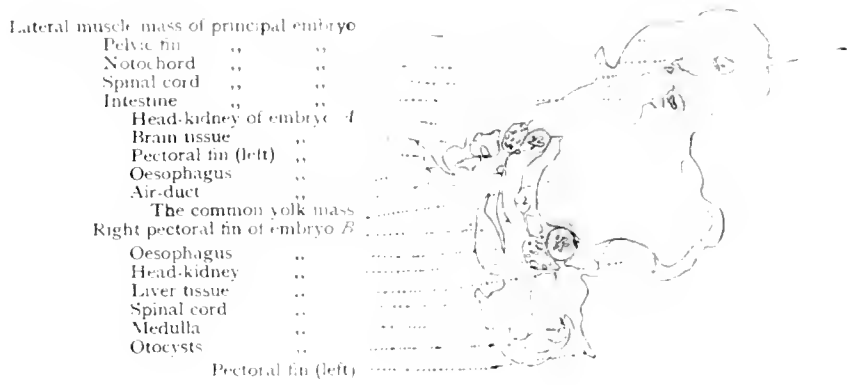
LETTERING IN ALL THE FIGURES.

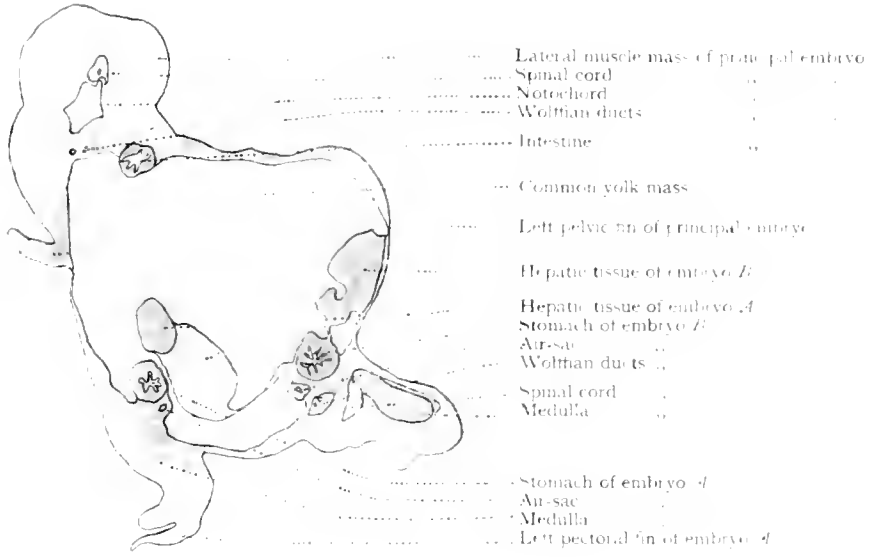
a	olfactory capsular cartilage.	*ff'*	outer and inner palato pterygoids.
b	trabeculæ cranii.	*gg'*	,, ,, hyomandibulars.
c	parachordal cartilages.	*kk'*	,, ,, periotic cartilages.
d	on trabeculæ in front of the two pituitary spaces.	*m*	in the two pituitary spaces.
e	on parachordals behind the pituitary spaces and the tendon of insertion of the M.	*ss'*	outer and inner Meckel's bars.
		hh'	,, ,, hyoid arches.

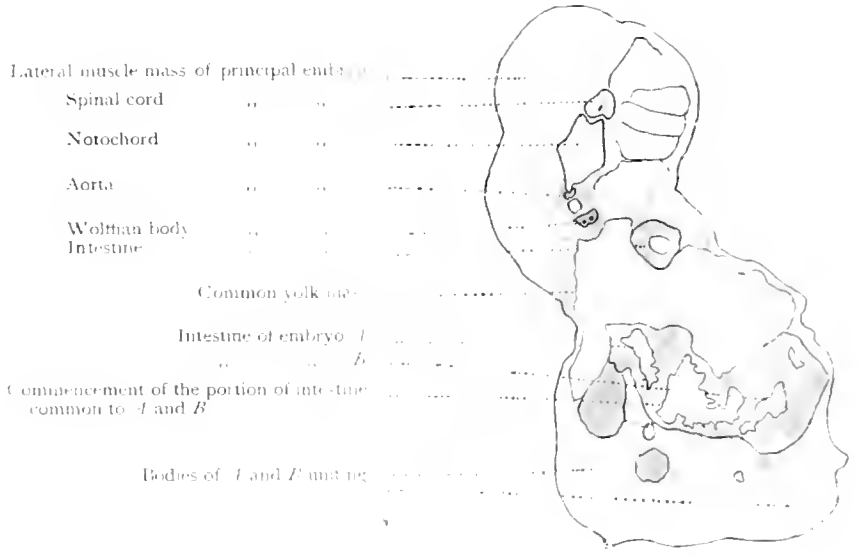
FIG. 94.—Sketch of triple monster trout embryo described on pp. 33, 34, as seen from the left side of the principal embryo. Between the latter and embryo *A* are two vents close together, while the single urinary pore is behind the vents. A marked keel along the left side of the composite tail is formed by fusion of the ventral edge membranes of these two embryos. A similar keel occurs along the right side, and is derived from the fusion of corresponding elements belonging to the principal embryo and to embryo *B*. The lower angle of the composite tail is formed by the fusion of the dorsal edge membranes of *A* and *B*. The specimen is also illustrated in the two succeeding figures and in Pl. VII, figs. 32-34, and Pl. XXIII figs. 07-09. (×6.)

FIG. 95.—Diagram of alimentary canals of the triple monster illustrated above. The whole canal of the principal embryo is quite separate from the canals of the other two, and has its own air-duct, air-sac, liver and bile-duct. The two defective embryos have the anus and last part of the intestine in common, but their gullets, stomachs, first portions of intestine, and liver outgrowths are separate. Other references are given under Fig. 94.

FIG. 96. Diagram of the urinary apparatus in the triple monster. The head-kidneys and, for the greater part of their length, the Wolffian ducts are separate, but there is only a single bladder and urinary pore. The left duct of the principal embryo, and the right duct of embryo *A*, unite before opening into this bladder, as also do the left duct of *A*, and the right duct of *B*. The left duct of *B* ends blindly. Other references are given under Fig. 94.


Lateral muscle mass of principal embryo
Pelvic fin ,, ,,
Notochord ,, ,,
Spinal cord ,, ,,
Intestine ,, ,,
Head-kidney of embryo A
Brain tissue ,,
Pectoral fin (left) ,,
Oesophagus ,,
Air-duct ,,
The common yolk mass
Right pectoral fin of embryo B
Oesophagus ,,
Head-kidney ,,
Liver tissue ,,
Spinal cord ,,
Medulla ,,
Otocysts ,,
Pectoral fin (left)


Lateral muscle mass of principal embryo
Spinal cord ,,
Notochord ,,
Wolffian ducts ,,
Intestine ,,
Common yolk mass
Left pelvic fin of principal embryo
Hepatic tissue of embryo B
Hepatic tissue of embryo A
Stomach of embryo B
Air-sac ,,
Wolffian ducts ,,
Spinal cord ,,
Medulla ,,
Stomach of embryo A
Air-sac ,,
Medulla ,,
Left pectoral fin of embryo A


Lateral muscle mass of principal embryo
Spinal cord ,, ,,
Notochord ,, ,,
Aorta ,, ,,
Wolffian body ,,
Intestine
Common yolk mass
Intestine of embryo A
,, ,, B
Commencement of the portion of intestine common to A and B
Bodies of A and B uniting

Lateral muscle mass of principal embryo
Pelvic fin ,, ,,
Notochord ,, ,,
Spinal cord ,, ,,
Intestine ,, ,,
Head-Kidney of embryo A
Brain tissue ,,
Pectoral fin (left) ,,
Oesophagus ,,
Air-duct ,,
The common yolk mass
Right pectoral fin of embryo B
Oesophagus ,,
Head-kidney ,,
Liver tissue ,,
Spinal cord ,,
Medulla ,,
Otocyst ,,
Pectoral fin (left)

Lateral muscle mass of principal embryo
Spinal cord
Notochord
Aorta
Wolffian body
Intestine
Common yolk mass
Intestine of embryo A
Commencement of the portion of intestine common to A and B
Bodies of A and B mating

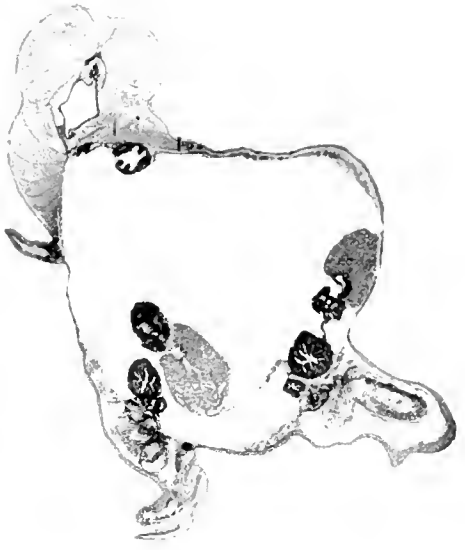
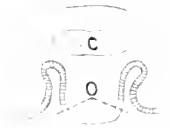


FIG. 68.—Transverse section belonging to the same series as the last figure, but a little further back. The body of embryo *A* is taken up chiefly with the nerve tissue of the medulla and spinal cord, while *B* shows a section of the tiny fourth ventricle and medulla. Below the bodies of *A* and *B* are seen the Wolffian ducts, urosteles, stomachs, and the hepatic tissue belonging to these embryos. A pelvic fin of the principal embryo comes into the section on its left side. Other references are given under Fig. 64. (× 14.)

FIG. 69.—Transverse section from same series as the last two figures, but at a considerable distance further back. The bodies of the two defective embryos are now uniting, and they are seen to be made up of very irregular tissues, the spinal cords being hardly recognisable. The intestinal canals of these embryos are joining together, the part seen towards the middle being the commencement of the common terminal portion. References under fig. 64. (× 17.)

100.



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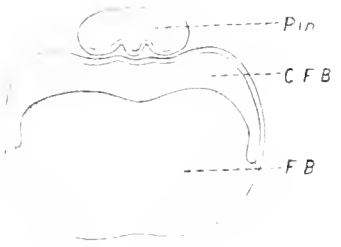
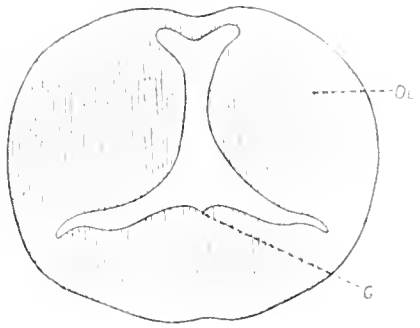
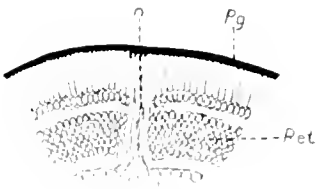


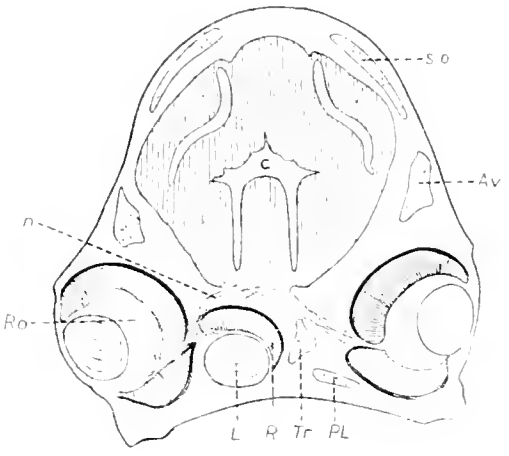
102



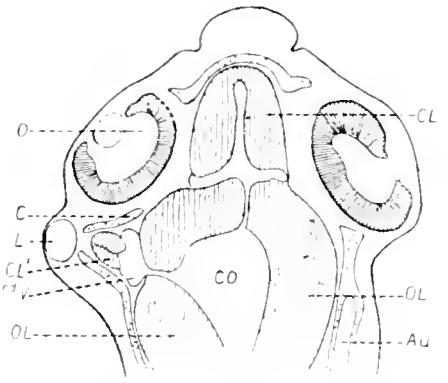
103.



104.



105.



106.

PLATE XXIV

FIG. 100.—Cyclopic trout embryo of type A (p. 40), seen from left side and showing the large single eye overarched by the mesial frontal process.

FIG. 101.—Transverse section of the frontal process referred to above, showing the small approximated olfactory pits (*o*), and the reduced olfactory capsular cartilage (*C*).

FIG. 102.—Transverse section through the posterior parts of the cerebral lobes in the same specimen, showing the pineal diverticulum (*Pin.*), and the cerebral lobes (*F.B.*), the latter being intimately united along their inner surfaces. The central cavity of the brain (*C.F.B.*) is not markedly dropsical, and the cerebral lobes are almost normal in their transverse measurements (p. 41).

FIG. 103.—Section through mid-brain of a cyclopic trout embryo belonging to type B (p. 41), showing almost complete obliteration of the mid-ventral groove which should lead downwards into the infundibulum. Infundibulum and hypophysis are absent.

FIG. 104.—Section through back part of retina of cyclopic eye (type B) described on p. 42, showing failure of development on the part of optic nerve and choroidal fissure. *Pg.* . . . hexagonal pigment layer; *Ret.* . . . retina; *n* . . . a few nerve fibres not perforating the pigment layer.

FIG. 105.—Transverse section of head of trout embryo with supernumerary eye (see p. 59).

L. Lens of supernumerary eye.
R. Retina " "
R.O. Right normal eye.
N. Right optic nerve receiving fibres from retina of supernumerary eye.
C. Central cavity of brain with two deep grooves in its floor, each of which leads downwards into an infundibulum and a hypophysis.
Tr. Trabeculae cranii displaced towards left.
P.Q. Palato-quadrate bar on left side; the right bar is absent.
S.o. Supra-orbital bar.
Au. Anterior corner of auditory capsular cartilage.

FIG. 106.—Horizontal section of head of trout embryo with supernumerary eye (see p. 60).

L. Lens belonging to the left (aborted) twin head.
CL'. Cerebral lobes belonging to ditto.
3rd V. 3rd ventricle belonging to ditto.
C. Cranial cartilages belonging to ditto.
O. Functional left eye.
CL. Functional cerebral lobes.
CO. Cavity of optic lobes.
OL. Optic lobes.
Au. Auditory cartilage.

PLATE XXIV

FIG. 100.—Cyclopic trout embryo of type A (p. 40), seen from left side and showing the large single eye overarched by the mesial frontal process.

FIG. 101.—Transverse section of the frontal process referred to above, showing the small approximated olfactory pits (*o*), and the reduced olfactory capsular cartilage (*C*).

FIG. 102.—Transverse section through the posterior parts of the cerebral lobes in the same specimen, showing the pineal diverticulum (*Pine*) and the cerebral lobes (*F.B.*), the latter being intimately united along their inner surfaces. The central cavity of the brain (*C.F.B.*) is not markedly dropsical, and the cerebral lobes are almost normal in their transverse measurements (p. 41).

FIG. 103.—Section through mid-brain of a cyclopic trout embryo belonging to type B (p. 41), showing almost complete obliteration of the mid-ventral groove which should lead downwards into the infundibulum. Infundibulum and hypophysis are absent.

FIG. 104.—Section through back part of retina of cyclopic eye (type B) described on p. 42, showing failure of development on the part of optic nerve and choroidal fissure. *Pg.* . . . hexagonal pigment layer; *Ret.* . . . retina; *n* . . . a few nerve fibres not perforating the pigment layer.

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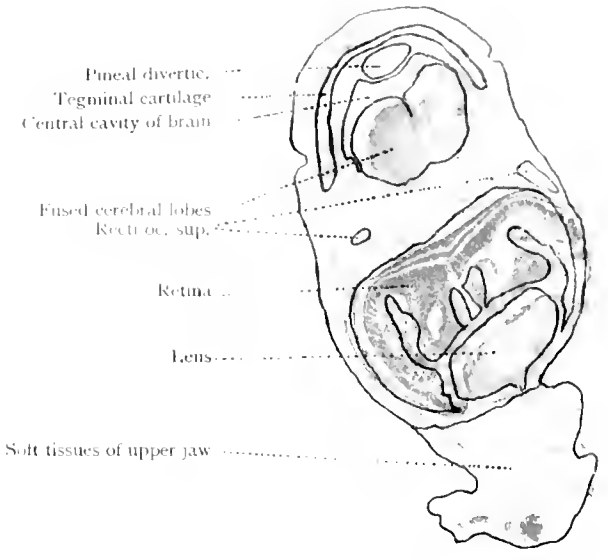
L. Lens of supernumerary eye.
R. Retina " "
R.O. Right normal eye.
N. Right optic nerve receiving fibres from retina of supernumerary eye.
C. Central cavity of brain with two deep grooves in its floor, each of which leads downwards into an infundibulum and a hypophysis.
Tr. Trabeculae cranii displaced towards left.
P.L. Palato-quadrate bar on left side; the right bar is absent.
S.o. Supra-orbital bar.
An. Anterior corner of auditory capsular cartilage.

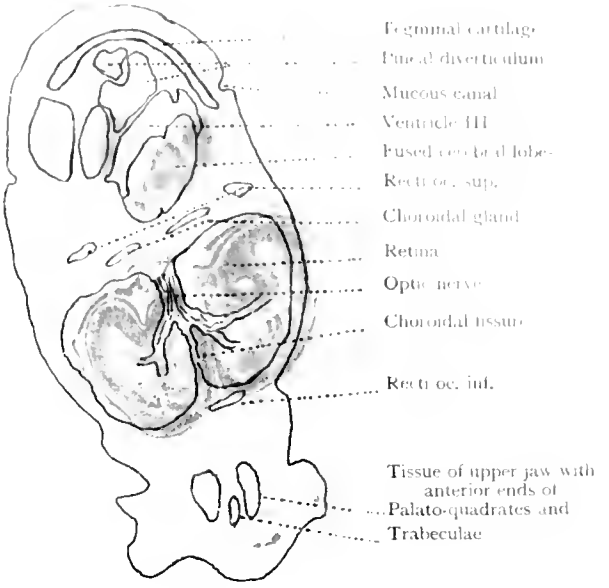
FIG. 106.—Horizontal section of head of trout embryo with supernumerary eye (see p. 60).

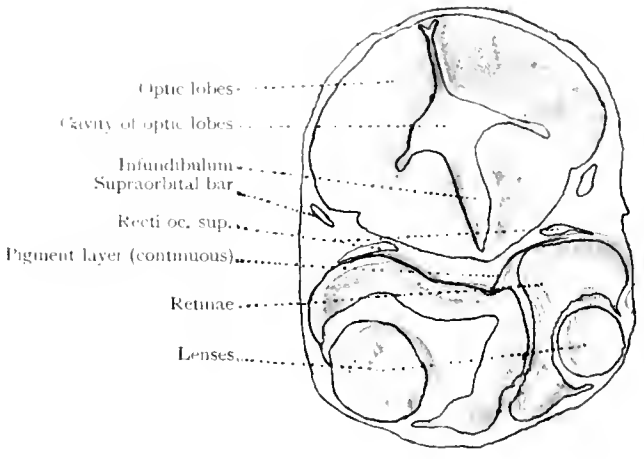
L. Lens belonging to the left (aborted) twin head.
CL. Cerebral lobes belonging to ditto.
3rd V. 3rd ventricle belonging to ditto.
C. Cranial cartilages belonging to ditto.
O. Functional left eye.
CL. Functional cerebral lobes.
CO. Cavity of optic lobes.
OL. Optic lobes.
An. Auditory cartilage.

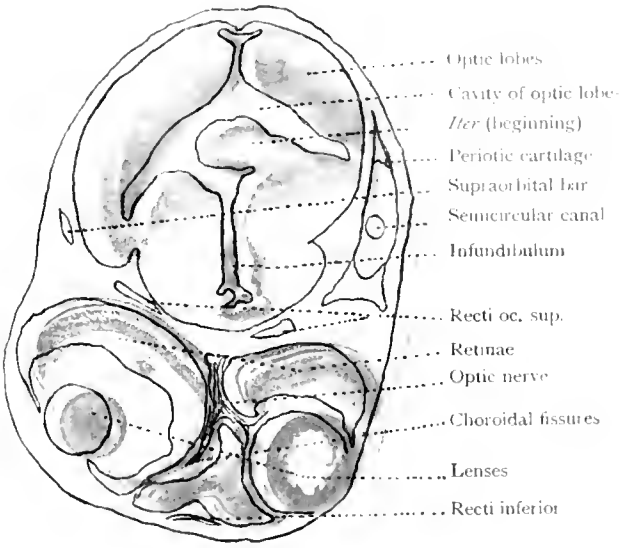
105

106


Pineal diverticulum
Tegminal cartilage
Central cavity of brain
Fused cerebral lobes
Recti oc. sup.
Retina
Lens
Soft tissues of upper jaw


Tegminal cartilage
Pineal diverticulum
Mucous canal
Ventricle III
Fused cerebral lobes
Recti oc. sup.
Choroidal gland
Retina
Optic nerve
Choroidal tissue
Recti oc. inf.
Tissue of upper jaw with anterior ends of
Palato-quadrates and
Trabeculae


Optic lobes
Cavity of optic lobes
Infundibulum
Supraorbital bar
Recti oc. sup.
Pigment layer (continuous)
Retinae
Lenses

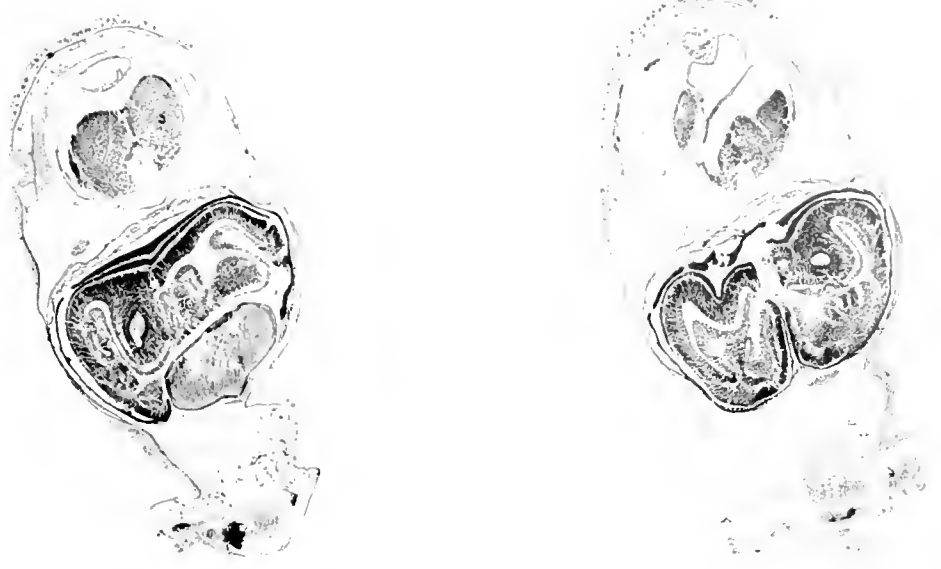

Optic lobes
Cavity of optic lobes
Iter (beginning)
Periotic cartilage
Supraorbital bar
Semicircular canal
Infundibulum
Recti oc. sup.
Retinae
Optic nerve
Choroidal fissures
Lenses
Recti inferior

Tegmental cartilage
Pineal diverticulum
Mucous canal
Ventricle III
Fused cerebral lobes
Rect oc. sup.
Choroidal glands
Retina
Optic nerve
Choroidal tissues
Recti oc. inf.
Tissue of upper jaw with anterior ends of Palato-quadrates and Trabeculae

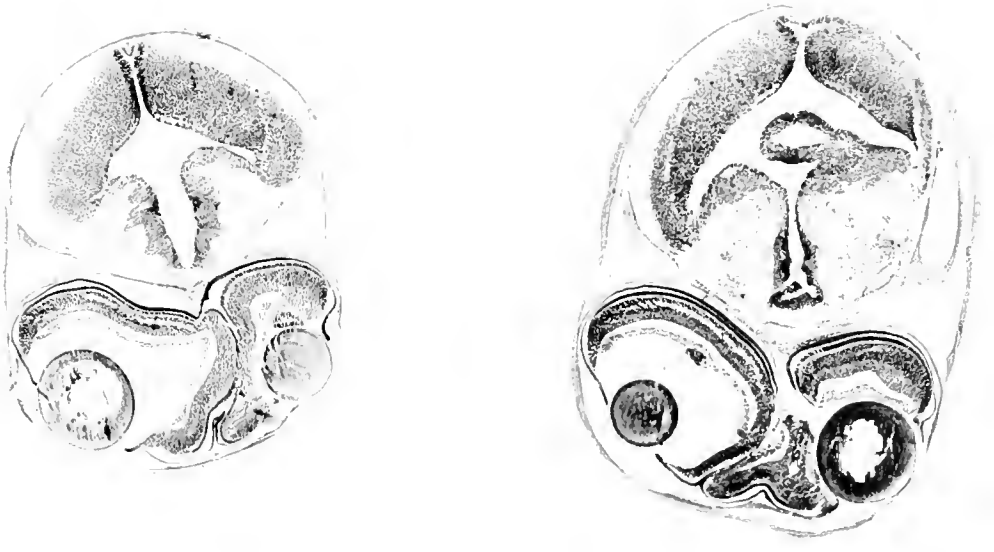
Pineal diverticulum
Tegmental cartilage
Central cavity of brain
Fused cerebral lobes
Recti oc. sup.
Retina
Lens
Soft tissue of upper jaw

Optic lobes
Cavity of optic lobes
Infundibulum
Supraorbital bar
Semicircular canal
Recti oc. sup.
Retinae
Optic nerve
Choroidal tissues
Lenses
Recti inferior

Optic lobes
Cavity of optic lobes
Infundibulum
Supraorbital bar
Recti oc. sup.
Pigment layer (continuous)
Retinae
Lenses



FIGS. 107 and 108. Sections through head of a cyclopic trout embryo, the former through the middle of the median eye and its lens, and the latter through the entrance of the single optic nerve. This nerve is seen to divide at once into two branches for the two partly separate retinæ. The fused condition of the cerebral lobes will be noted, particularly in Fig. 107. For details of structure see pp. 40-42. Compare also with the two succeeding figures, and with Pl. XXVI, fig. 111. (× 24.)



FIGS. 109 and 110. Transverse sections of the head of a trout embryo showing the condition of semi-cyclopia. There are two eyes, but they are close together, and the optic nerve is single, although there are two choroidal fissures. The internal recti are absent. As in typical cyclopia, the eyes intervene between the base of the brain and the trabeculæ cranii, the anterior ends of which are separated by a wide gap from the rudimentary olfactory capsular cartilages. The latter are not shown in this section. Compare with the two preceding figures, and with Pl. XXVI, fig. 111. See also p. 44. (× 24.)

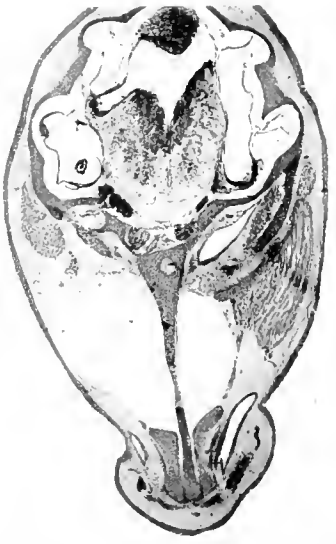


FIG. 111.—Section through head of a semi-cyclopic trout embryo, from same series as Pl. XXV. figs. 109, 110, but further back in the series. The section passes almost horizontally along the trabeculae cranii, which here form a single mesial rod. See pp. 40, 44. Anteriorly, the trabeculae are seen to articulate with the palato-pterygoids; behind them the two external recti of the eye are passing through the pituitary space in company with the two choroidal arteries. The head is somewhat compressed in the sagittal plane. (× 24.)

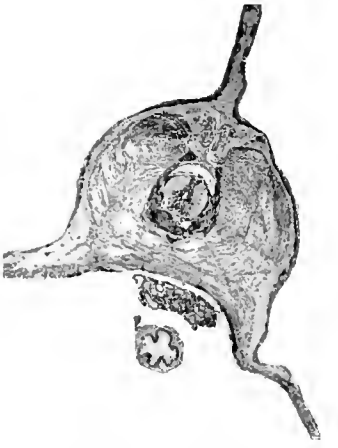


FIG. 113.—Transverse section of body of trout embryo just behind the pectoral fins, showing local absence of the notochord. The adjacent neural and haemal arch cartilages fuse together to form a series of half rings below the spinal cord. The lateral muscles meet in a mesial raphe above the dorsal aorta and below the spinal cord. See p. 54. (× 20.)

FIG. 112.—Transverse section through atrophic head of an embryo trout, in which the lenses alone of all the eye structures have survived. Even the mouth, the Meckel's cartilages, the trabeculae, and the palato-pterygoids are absent. See pp. 60, 61. (× 16.)

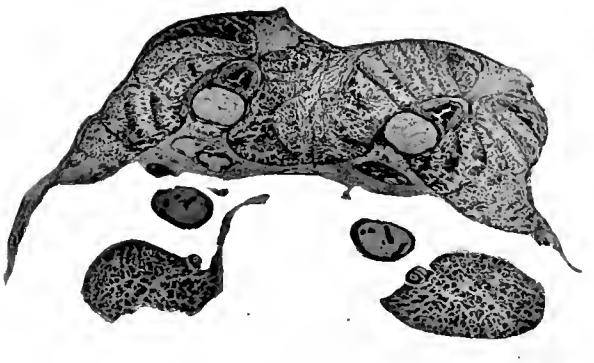
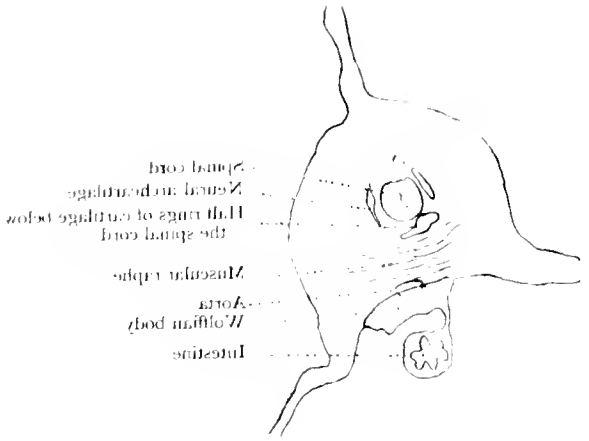
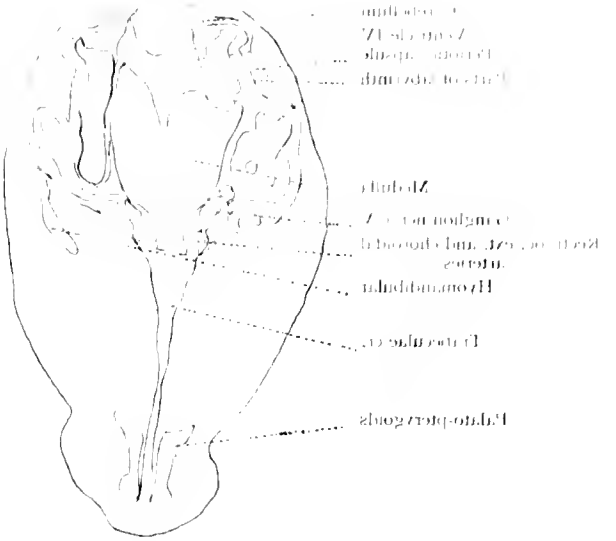
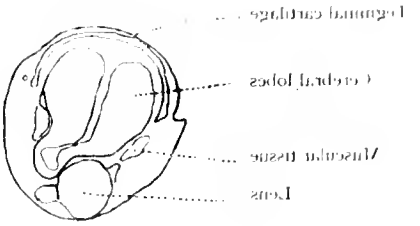


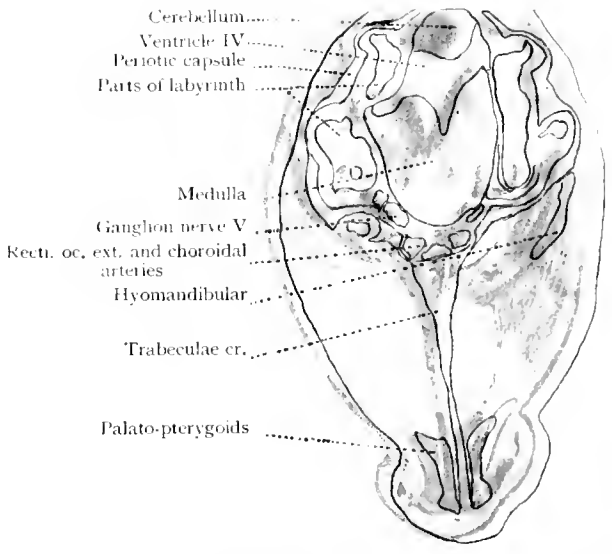
FIG. 114.—Transverse section of double monster belonging to the type described under Class V. on pp. 20-21. The section passes across the middle of the body, and shows the twin sets of structures coming together to unite in lateral union. The intestinal canals are here separate, as also are the livers, air-sacs, Wolffian bodies, etc. (× 16.)

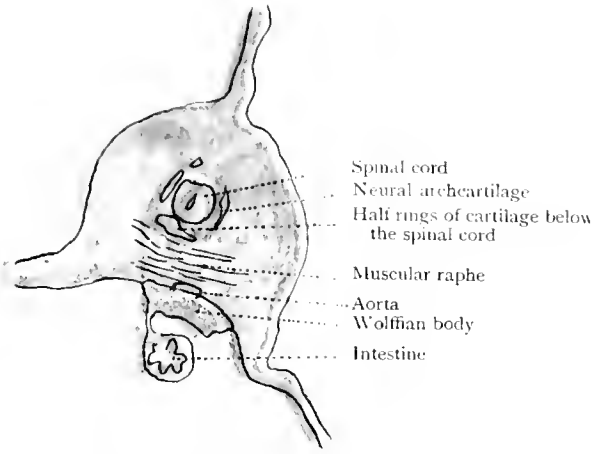

Spinal cord
Neural archeartilage
Half rings of cartilage below the spinal cord
Muscular raphe
Aorta
Wolffian body
Intestine

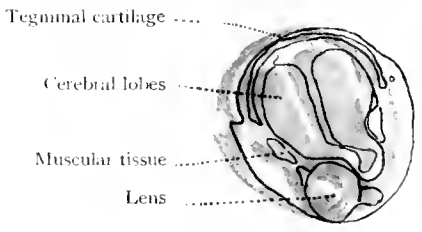

Medulla
Hyomandibular
Palato-pterygoids

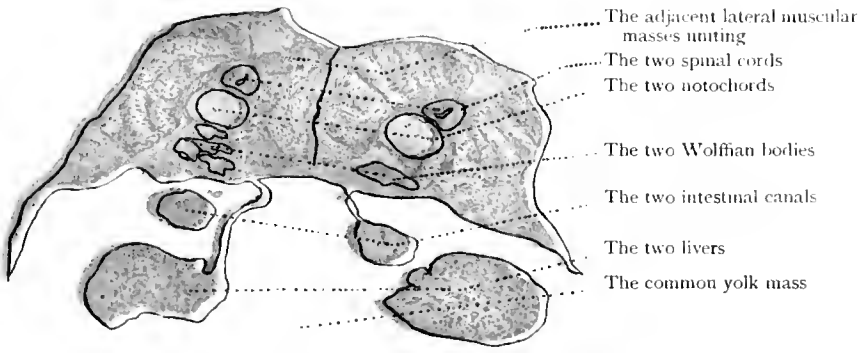
The adjacent lateral muscular masses uniting
The two spinal cords
The two notochords
The two Wolffian bodies
The two intestinal canals
The two livers
The common yolk mass


Cerebral lobes
Muscular tissue
Lens


Cerebellum
Ventricle IV
Periotic capsule
Parts of labyrinth
Medulla
Ganglion nerve V
Rectt. oc. ext. and choroidal arteries
Hyomandibular
Trabeculae cr.
Palato-pterygoids


Spinal cord
Neural archcartilage
Half rings of cartilage below the spinal cord
Muscular raphe
Aorta
Wolffian body
Intestine


Tegmmal cartilage
Cerebral lobes
Muscular tissue
Lens


The adjacent lateral muscular masses uniting
The two spinal cords
The two notochords
The two Wolffian bodies
The two intestinal canals
The two livers
The common yolk mass